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The Cenomanian and Turonian (mid-Cretaceous) ammonite biostratigraphy of north-eastern Nigeria

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SYNOPSIS. The Cenomanian–Turonian ammonite biostratigraphy of the Pindiga Formation and its age equivalents was investigated at a number of localities in north-eastern Nigeria. Five biozones were found to be recognizable in the main limestone-bearing sequences of the region as a whole: a Zone of *Nigericeras gadeni* (Chudeau) at the base, a Zone of *Vascoceras cauvini* Chudeau, a Zone of *Vascoceras proprium* (Reyment), a Zone of *Pseudotissotia nigeriensis* (Woods) and a Zone of *Wrightoceras wallsi* Reyment above. The Gadeni and Cauvini Zones are Late Cenomanian in age while the Nigeriensis and Wallsi Zones are Early Turonian. The Cenomanian–Turonian boundary lies within or at the top of the Proprium Zone. The Wallsi Zone at Dukul is overlain by a condensed horizon containing *Fagesia* sp., *Neoptychites cephalotus* (Courtiller), *Wrightoceras munieri* (Pervinquière) and *Hoplitoides ingens* (von Koenen), ammonites ranging from Lower to Middle Turonian. The youngest Turonian zone recognizable is that of *Coilopoceras discoideum* Barber. A broadly similar ammonite succession occurs in the Algerian Sahara, while correlation of these Nigerian zones with those in Israel is good, especially in the Upper Cenomanian. Local subsidence history had a profound effect on the age, thickness and lithological character of the ammonite-bearing sequences in north-eastern Nigeria; all these factors vary significantly.

INTRODUCTION

The Cenomanian–Turonian limestones of north-eastern Nigeria have long been noted for their prolific vascoceratid-dominated ammonite faunas. Elements were first described by Woods (1911), but following the accounts of Reyment (1954, 1954*a*, 1955) and Barber (1957, 1960) the full wealth of these assemblages became evident. This area has subsequently assumed major importance in mid-Cretaceous Tethyan biostratigraphy. The ammonite-bearing beds outcrop widely but in its details the geology of the region is rather complex, a fact reflected by the multiplicity of lithostratigraphical and palaeogeographical terms applied to it. Cretaceous sedimentation in north-eastern Nigeria was, for its greater part, strongly influenced by a number of important strike-slip faults trending NE–SW (Benkhelil 1982, Benkhelil & Robineau 1983, Popoff *et al.* 1983, Maurin *et al.* 1986; Fig. 1). Two major sedimentary basins are present, the Chad Basin to the north and the Lau Basin (Benue Basin of Carter *et al.* (1963), Lamurde Basin of Ojo & Pinna (1982)), comprising the distal part of the Benue Trough, to the south. The area between, termed the 'Zambuk Ridge' by Carter *et al.* (1963), is characterized by strong faulting which resulted in the development of several differentially subsiding basins (Ojo & Pinna 1982, Maurin *et al.* 1986). Following the first systematic geological mapping of the region, Carter *et al.* (1963) referred the Cenomanian–Turonian limestone-shale sequence in the western part of the Chad Basin to the Gongila Formation, that in the Lau Basin to the Dukul Formation and that in the remaining area to the Pindiga Formation. These marine formations overlie a transitional sandstone-shale sequence (the Yolde Formation) over most of north-eastern Nigeria. The earliest sediments are a thick but varied fluviatile and

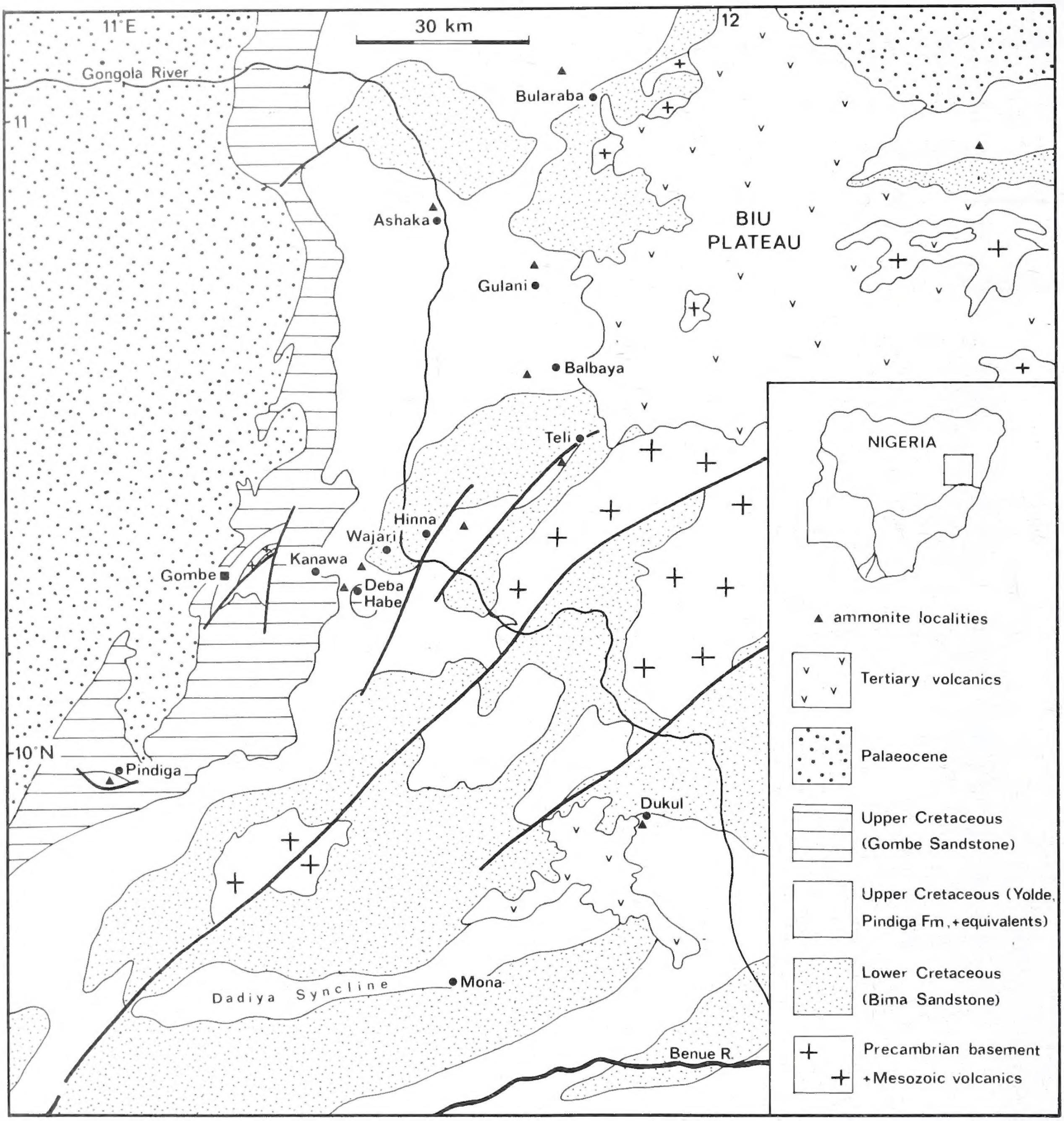

11°E
Gongola River
11
30 km
12
Bularaba
Ashaka
Gulani
Balbaya
BIU PLATEAU
Teli
Hinna
Wajari
Kanawa
Gombe
Deba
Habe
10°N
Pindiga
Dukul
Dadiya Syncline
Mona
Benue R.
NIGERIA
▲ ammonite localities
Tertiary volcanics
Palaeocene
Upper Cretaceous (Gombe Sandstone)
Upper Cretaceous (Yolde, Pindiga Fm,+equivalents)
Lower Cretaceous (Bima Sandstone)
Precambrian basement +Mesozoic volcanics

Fig. 1 Simplified geological map of part of north-eastern Nigeria showing ammonite localities mentioned in the text.

lacustrine succession, the Bima Sandstone of Aptian to Albian age (Allix *et al.* 1981, Doyle *et al.* 1982) which underlies the entire area.

Woods (1911) established the presence of Turonian deposits in north-eastern Nigeria but Reyment (1954) proposed the first subdivision of this stage in Nigeria, regarding the vascoceratid-dominated faunas as characteristic of his 'Oldest Beds' (of the Turonian). These beds he subsequently referred to as the 'Zone of *Pachyvascoceras costatum* Reyment' and, later, as the 'Zone of *Pseudotissotia* (*Wrightoceras*) *wallsi* Reyment' (Reyment 1956, 1965). Barber (1957), however, proposed three zones for this sequence in north-eastern Nigeria: a Zone of *Vascoceras bulbosum* (Reyment) below, a Zone of *Paravascoceras costatum* (Reyment) and a Zone of *Pseudotissotia* (*Bauchioceras*) *nigeriensis* above. All were assigned to the Lower Turonian, though Barber noted the Cenomanian affinities of elements of his Bulbosum Zone fauna. Wozny & Kogbe (1983) later proposed a 'Zone of *Gombeoceras gongilense* Reyment' between Barber's Costatum and Nigeriensis Zones. These three zones they referred to the Lower Turonian, regarding Barber's Bulbosum Zone as Upper Cenomanian. Most recently, Popoff *et al.* (1986) reinvestigated the Gongila Formation at Ashaka Quarry and the Pindiga Formation at its streamside type locality (see Fig. 1). They divided the ammonite-bearing levels into seven zones, as follows:

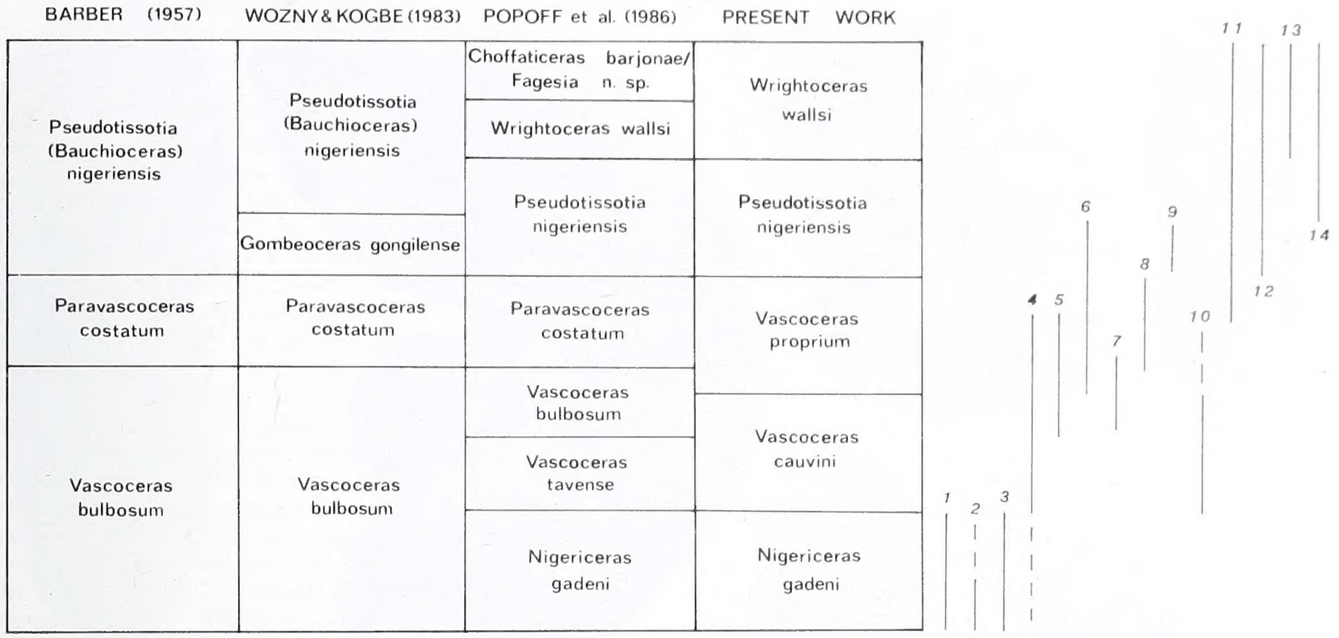


Fig. 2 Present and previous proposals for a biostratigraphical subdivision of the Upper Cenomanian and Lower Turonian in north-eastern Nigeria based on ammonites. The stratigraphical ranges of selected forms are shown at right: 1, *Metengonoceras dumbli*. 2, *Metoicoceras geslinianum*. 3, *Nigericeras gadeni*. 4, *Vascoceras cauvini*. 5, *V. nigeriense*. 6, *V. proprium*. 7, *V.* sp. juv. 8, '*Paramammites*' sp. 9, *Pseudaspidoceras* cf. *flexuosum*. 10, *P.* cf. *pseudonodosoides*. 11, *Thomasites gongilensis*. 12, *Pseudotissotia nigeriensis*. 13, *Wrightoceras wallsi*. 14, *Eotissotia simplex*.

7. Zone of *Choffaticeras barjonae* (Choffat)/*Fagesia* n. sp. (youngest)
6. Zone of *Wrightoceras wallsi*
5. Zone of *Pseudotissotia nigeriensis*
4. Zone of *Paravascoceras costatum*
3. Zone of *Vascoceras bulbosum*
2. Zone of *Vascoceras tavense* Faraud
1. Zone of *Nigericeras gadeni* (Chudeau) (oldest).

Zones 1–3 were dated Late Cenomanian, the Costatum Zone Early Turonian and zones 5–7 Middle Turonian.

There has, therefore, been a divergence of opinion regarding the biostratigraphical subdivision and precise ages of these beds. One of the main problems in dealing with vascoceratid faunas is ascertaining the limits of individual species which are frequently represented by a large array of morphotypes (see, for example, Schöbel 1975, Renz 1982, Hirano 1983, Berthou *et al.* 1985, Kennedy *et al.* 1987). The taxonomic approaches adopted by previous authors have strongly influenced their biostratigraphical and palaeobiogeographical interpretations of the Nigerian faunas. The purpose of this contribution is not to attempt a complete taxonomic revision of these ammonites but rather to propose a biostratigraphy effective in correlation both within and outside north-eastern Nigeria. Inevitably, however, certain taxonomic remarks are necessary especially in regard to those species that have been selected as zonal indices.

PROPOSED BIOZONATION

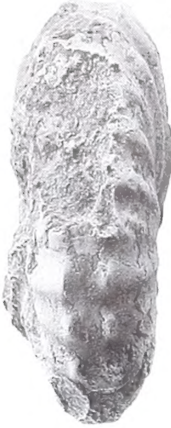
The following ammonite biozones are proposed for the main part of the Late Cenomanian and Early Turonian limestone-bearing sequences in north-eastern Nigeria:

5. Zone of *Wrightoceras wallsi* (youngest)
4. Zone of *Pseudotissotia nigeriensis*
3. Zone of *Vascoceras proprium* (Reyment)
2. Zone of *Vascoceras cauvini* Chudeau
1. Zone of *Nigericeras gadeni* (oldest).

This scheme has been found to be applicable over the region as a whole. Zones 1–4 are interval zones, defined at their bases by the appearances of the index species. Zone 5 is a range zone based on the local occurrence of *W. wallsi*. The relationship of these zones to previously proposed schemes is shown in Fig. 2. As discussed below, the Wallsi Zone is locally overlain by a fauna containing, amongst others, *Hoplitoides*. At Mona and Bularaba (Fig. 1) still younger Turonian beds contain *Coilopoceras discoideum* Barber.

The *Nigericeras gadeni* Zone

A Zone of *Nigericeras gadeni* was first proposed by Popoff *et al.* (1986) for the earliest ammonite-bearing beds in north-eastern Nigeria. Although ammonites are generally scarce in this zone, *N. gadeni* occurs in some numbers and has a wide geographical distribution in the region. In this study it has not been found outside the Gadeni Zone, but Popoff *et al.* (1986: 348) reported it from Ashaka Quarry as high as beds included here in the *Vascoceras proprium* Zone. Faunas characteristic of the Gadeni Zone can be recognized in the lowest limestone bed at Pindiga (unit 1 of Barber 1957: table 3; unit 3 of Popoff *et al.* 1986: 354); at Ashaka Quarry (units 2 and 3 of Popoff *et al.* 1986: 347; the former, contrary to their statement, being exposed in a drainage cut in the eastern part of the quarry); in the lowest limestone bed exposed at Deba Habe; in the region between Kanawa and Hinna; at Teli; and to the north-east of the Biu basalt plateau (see Fig. 1). At the last two localities the Gadeni Zone is the only ammonite biozone present.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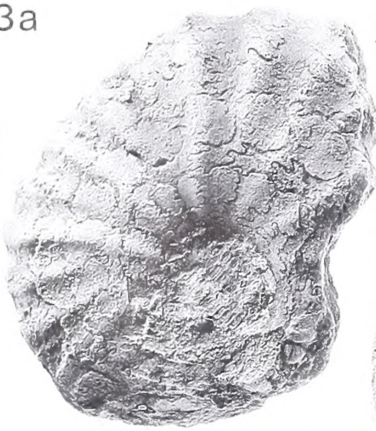
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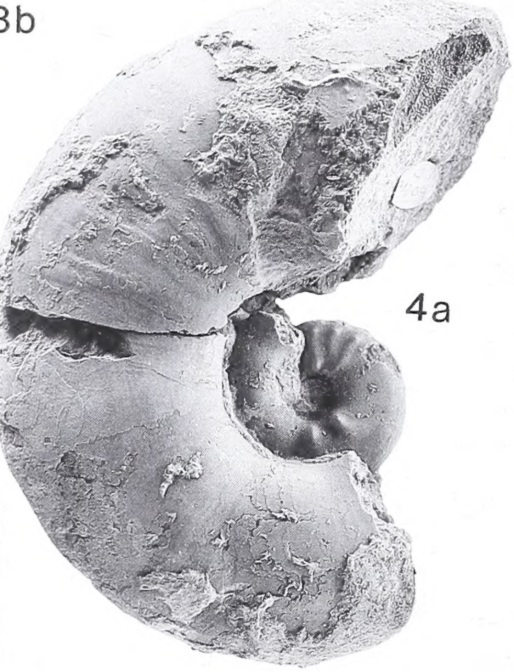
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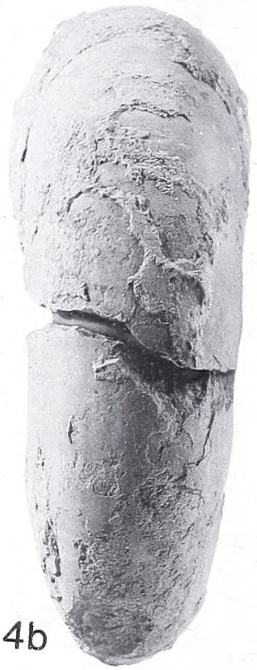
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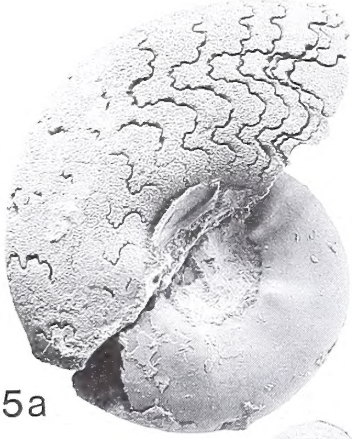
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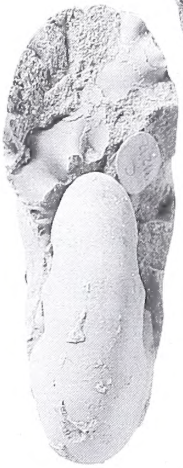
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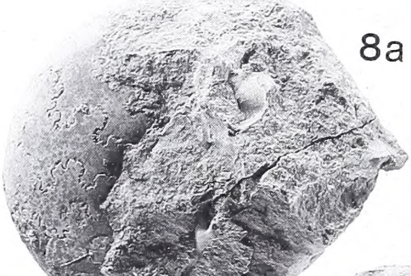
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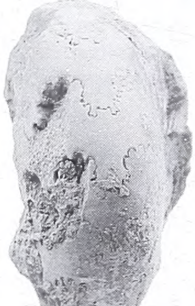
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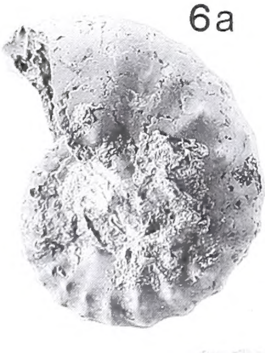
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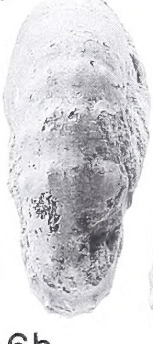
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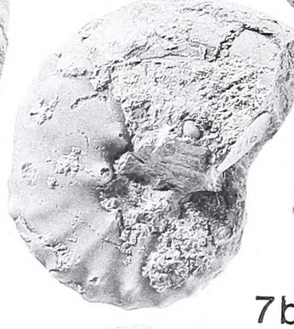
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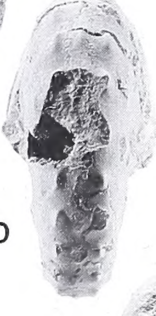
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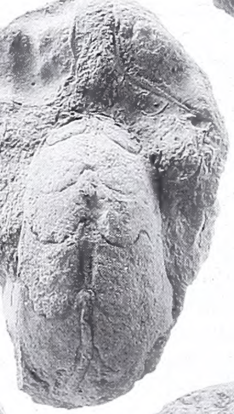
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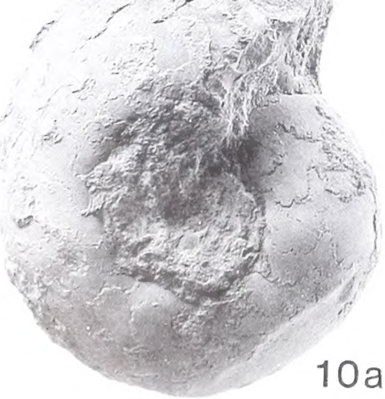
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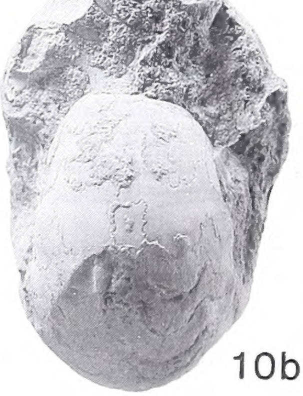
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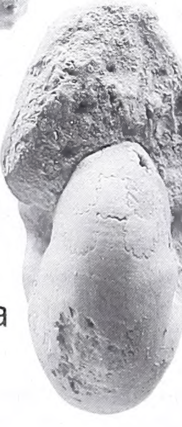
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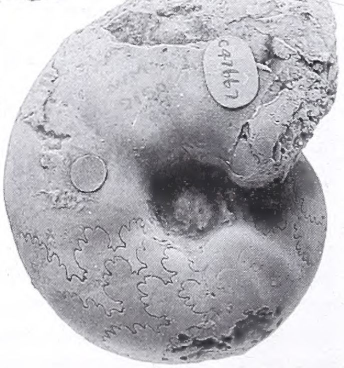
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Material of *N. gadeni* from north-east Nigeria is variable as regards strength and persistence of the juvenile ornamentation (Figs 4–7). Numerous specimens resemble in particular *N. lamberti* Schneegans (1943: 121; pl. 6, figs 1–5, 7). In agreement with Schöbel (1975) and Wright & Kennedy (1981), *N. lamberti*, *N. gignouxi* Schneegans (1943: 119; pl. 5, figs 10–15) and *N. jacqueti* Schneegans (1943: 125; pl. 6, fig. 8; pl. 7, fig. 1) are here regarded as synonyms of *N. gadeni* (Chudeau 1909: 71; pl. 3, fig. 6), making up a series varying mainly in the ornamental details mentioned above. The Gadeni Zone has also yielded *Metengonoceras dumbli* (Cragin) at Pindiga and Deba Habe. East of Kanawa a single specimen of *Metoicoceras geslinianum* (d'Orbigny) (Fig. 3) was found in scree which otherwise produced only rare *Metengonoceras dumbli*, more frequent *Nigericeras gadeni* and a poorly preserved fragment of *Vascoceras*. A fragment of a compressed *Vascoceras*, perhaps referrable to *V. cauvini*, was also found in the lowermost limestone bed at Pindiga. Two further, rather better preserved, immature specimens of *Vascoceras* (Figs 9, 10) were collected from the same bed. One of these (Fig. 10) shows broad, clavate umbilical tubercles similar to those discernible in the holotype of *V. bulbosum* (Reyment 1954*a*: pl. 4, figs 2a, b). The Pindiga individual is more inflated but is linked to the latter specimen by an ammonite referred to *V. bulbosum* by Barber (1957: pl. 6, fig. 8; Fig. 11 here). The Pindiga material mentioned above may be conspecific with *V. bulbosum* which itself is a possible synonym of *V. cauvini* Chudeau (see below). If *V. cauvini* is confirmed at this stratigraphical level in Nigeria, the Cauvini Zone can be extended downwards to include those beds here referred to as the Gadeni Zone, with the latter possibly being retained as a subzone. Popoff *et al.* (1986) reported *Eotissotia* Barber from the Gadeni Zone at Pindiga. This genus is otherwise found only at much higher stratigraphical levels in the Nigeriensis and Wallsi Zones. Finally, a fragment of a depressed ammonite with an acanthoceratid ornament (British Museum (Natural History) C.91294), possibly referrable to *Euomphaloceras*, was found in the Gadeni Zone at Pindiga.

The *Vascoceras cauvini* Zone

The base of this zone is marked by the appearance of *Vascoceras cauvini*, which can at present be drawn in the middle of unit 3 of Barber (1957: table 3), that is unit 4 of Popoff *et al.* (1986: 354), at Pindiga, and at the base of unit 4 of Popoff *et al.* (1986: 348) at Ashaka. It encompasses the greater part of the '*Vascoceras bulbosum* Zone' of Barber (1957) and the '*Vascoceras tavense* Zone' and lower part of the '*Vascoceras bulbosum* Zone' of Popoff *et al.* (1986) (see Fig. 2).

The Cauvini Zone is characterized by the common occurrence of moderately involute, compressed *Vascoceras*, generally smooth or nearly so in the juvenile whorls but sometimes with broad umbilical bullae. Such forms were referred by Barber (1957) to *V. bulbosum* (see Barber 1957: pl. 6, figs 6, 8) and *V. depressum* Barber (1957: 19; pl. 6, fig. 5). Only immature specimens have been found at Pindiga (Figs 8, 15). At other localities, notably Ashaka Quarry, the later growth stages are well represented and show the characteristic ventral ribbing of *V. cauvini* Chudeau (1909: 68; pls 1–2; pl. 3, figs 1, 2, 4) to which these specimens are here referred. A series of specimens at different growth stages is shown in Figs 12–14. *V. bulbosum* itself is based on a rather more inflated specimen than these (C.47295; see Reyment 1954*a*: pl. 4, figs 2a, b) showing broad, clavate umbilical ornamentation. It is, however, closely matched in whorl proportions by a specimen from Damergou included in *V. cauvini* by Chudeau (1909: pl. 3, figs 4a, b). This individual was refigured by Schneegans (1943: pl. 4, fig. 1) as *Paravascoceras nigeriensis* (Woods), apparently because of its early loss of umbilical tuberculation. Both Reyment (1954*a*: 256) and Barber (1957: 15) also tentatively referred it to this species. Contrary to the impression given by Woods (1911), however, rapid loss of ornamentation is by no means a characteristic feature of *Vascoceras nigeriense*. Certain specimens retain umbilical tubercles, often becoming bullate, to diameters of 70 mm or more (Fig. 25). It is possible that Chudeau's individual mentioned above is a true *V. cauvini* of which *V. bulbosum* may be a synonym. A list of further possible synonyms has been given by Schöbel (1975).

At Pindiga the uppermost part of the Cauvini Zone and the lowermost part of the overlying Proprium Zone consist of two thin calcareous beds separated by 50 cm of shales with gypsum (unit 5 of Barber 1957: table 3). These calcareous beds contain a stratigraphically important but taxonomically problematical assemblage of juvenile *Vascoceras* (Figs 17–18, 20). At Deba Habe a comparable association (Figs 16, 21) again occurs in an equivalent stratigraphical position. Barber (1957: 27) noted the similarity of some of these forms to *V. nigeriense* but, uncertain of their precise affinities, left them in open nomenclature as '*Vascoceras* sp. juv.' These individuals are consistently rather evolute and ventrally are either smooth or with only broad, low ribs. Their umbilical ornament, however, is highly variable. In some (Fig. 20) there are comparatively small, rounded umbilical tubercles. More commonly prominent, highly bullate umbilical tubercles are present, giving off single or paired indistinct ribs which fade over the venter (Figs 17, 21). This range of ornament is reminiscent of that in *Vascoceras diartianum* (d'Orbigny) (see Kennedy & Juignet 1977) and in particular of an assemblage from the Upper Cenomanian of southern Germany described by Förster *et al.* (1983: 133; pl. 3, figs 1–5). Others still show large, frequently paired, umbilical bullae (Fig. 18). Such massive tuberculation recalls that in *V. silvanense* Choffat (1898: 57; pl. 8, fig. 5; pl. 21, fig. 9), a form based on a juvenile of uncertain affinity (Berthou *et al.* 1985: 68). Although, within the Nigerian faunas, *V. nigeriense* is closest in whorl proportions to these juveniles, their variability precludes assignment to this species with confidence, if indeed they are all conspecific. It should also be noted that

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Figs 3a, b *Metoicoceras geslinianum* (d'Orbigny). Pindiga Formation (Gadeni Zone), between Kanawa and Wajari. C.91205, × 1.

Figs 4–7 *Nigericeras gadeni* (Chudeau). Pindiga Formation (Gadeni Zone). Figs 4a, b, C.91209, × 1. North-east of Biu plateau. Figs 5a, b, C.91212, × 1. Teli. Figs 6a, b, C.91215, × 1. Between Kanawa and Wajari. Figs 7a, b, C.91216, × 1. Between Kanawa and Wajari.

Figs 8a, b *Vascoceras cauvini* Chudeau. Pindiga Formation (Cauvini Zone), Pindiga. C.91285, × 1.

Figs 9, 10 *Vascoceras* sp. Pindiga Formation (Gadeni Zone), Pindiga. Fig. 9, C.91225, × 1. Figs 10a, b, C.91224, × 1.

Figs 11a, b *Vascoceras bulbosum* (Reyment). Pindiga Formation, Pindiga. C.47667, × 1 (see also Barber 1957: pl. 6, fig. 8).

All specimens are housed in the British Museum (Natural History), London.

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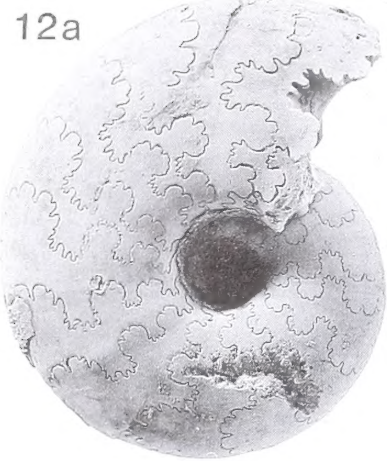

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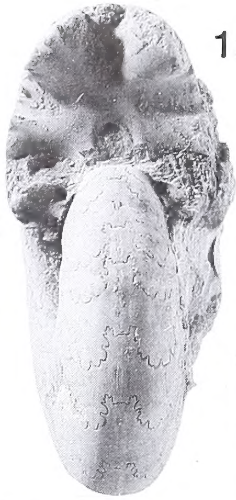

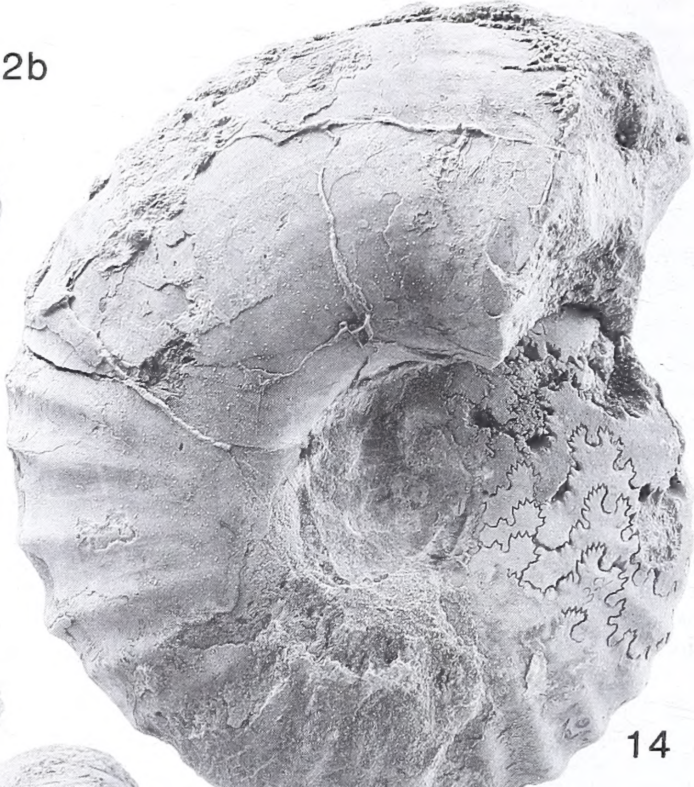
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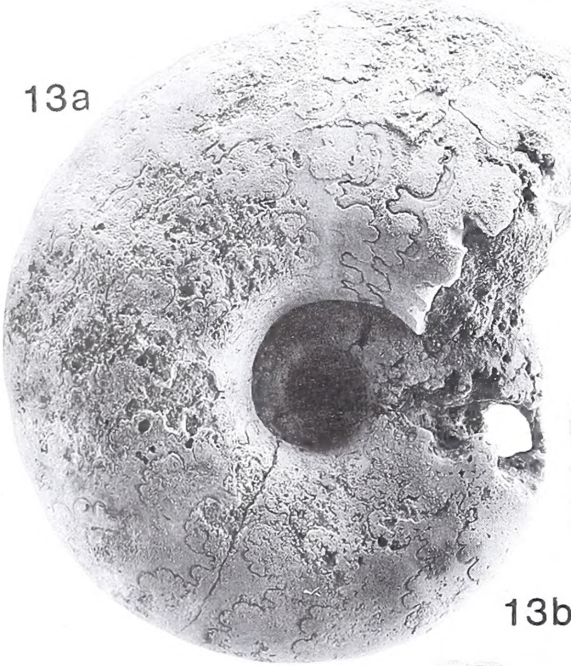

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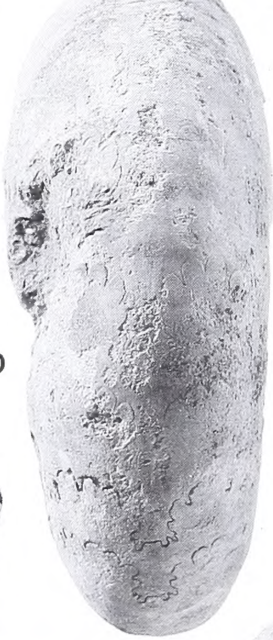

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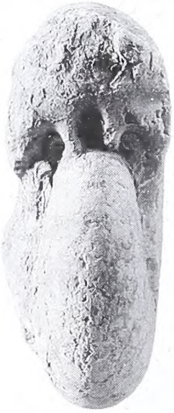

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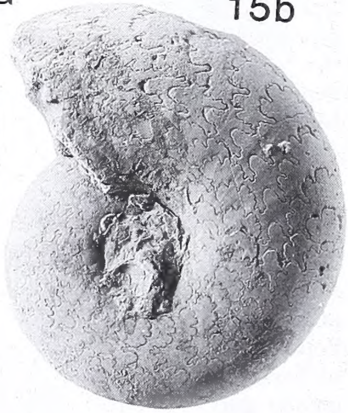

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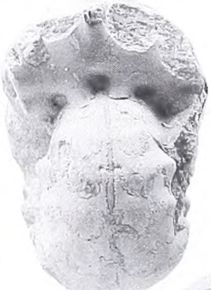

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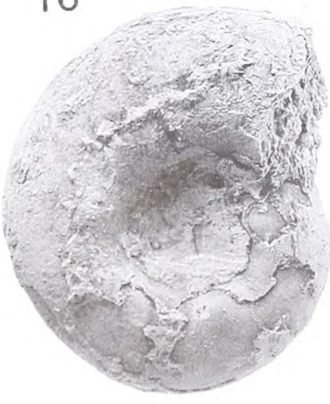

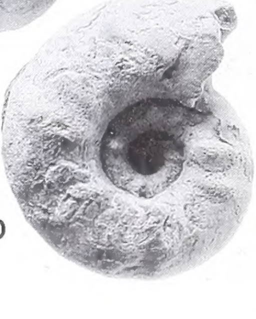
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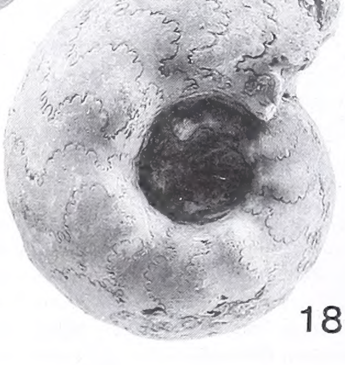
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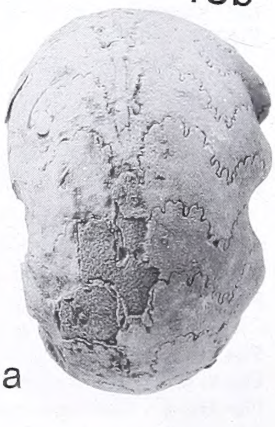

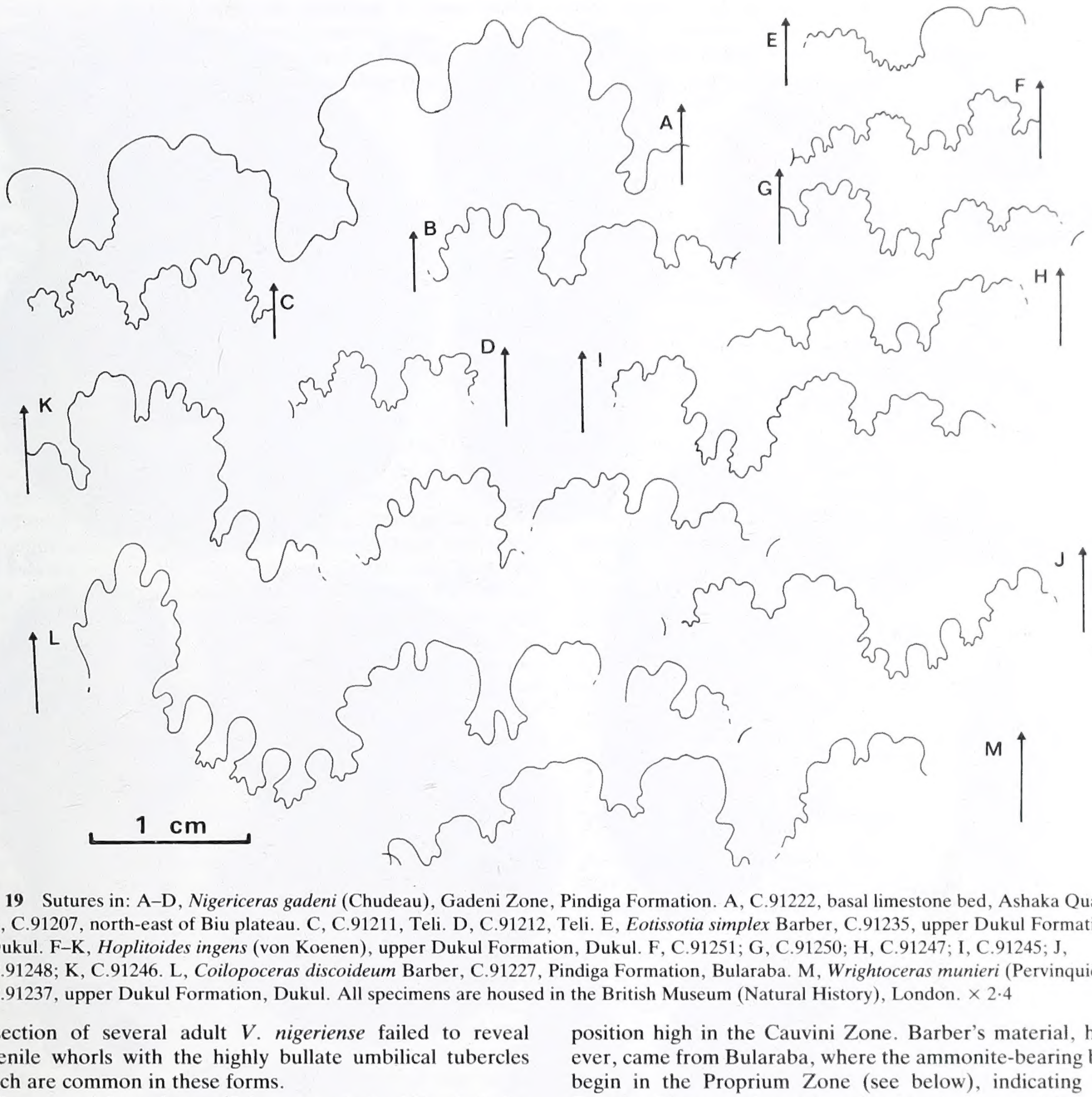

Fig. 19 Sutures in: A–D, *Nigericeras gadeni* (Chudeau), Gadeni Zone, Pindiga Formation. A, C.91222, basal limestone bed, Ashaka Quarry. B, C.91207, north-east of Biu plateau. C, C.91211, Teli. D, C.91212, Teli. E, *Eotissotia simplex* Barber, C.91235, upper Dukul Formation, Dukul. F–K, *Hoplitoides ingens* (von Koenen), upper Dukul Formation, Dukul. F, C.91251; G, C.91250; H, C.91247; I, C.91245; J, C.91248; K, C.91246. L, *Coilopoceras discoideum* Barber, C.91227, Pindiga Formation, Bularaba. M, *Wrightoceras munieri* (Pervinquière), C.91237, upper Dukul Formation, Dukul. All specimens are housed in the British Museum (Natural History), London. × 2·4

dissection of several adult *V. nigeriense* failed to reveal juvenile whorls with the highly bullate umbilical tubercles which are common in these forms.

Vascoceras cf. *evolutum* (Schneegans 1943: 130; pl. 8, fig. 2) is common in the Cauvini Zone at Ashaka and Pindiga; it occurs associated with *Pseudaspidoceras pseudonodosoides* (Choffat). At Dukul the stratigraphically lowest ammonite collected belongs to the latter genus (Fig. 22). This form is conspecific with the '*Pseudaspidoceras* sp.' of Barber (1957: 11; pl. 25, fig. 8) which, while losing all but the umbilical ornament early in ontogeny, shows the robust, rectiradiate ribbing of *P. pseudonodosoides* in its juvenile and middle growth stages. The Dukul specimen occurs below scree levels containing ammonites typical of the Proprium and Nigeriensis Zones (Fig. 28), suggesting a stratigraphical position high in the Cauvini Zone. Barber's material, however, came from Bularaba, where the ammonite-bearing beds begin in the Proprium Zone (see below), indicating that *Pseudaspidoceras* of *pseudonodosoides* type extend into this part of the sequence.

Popoff *et al.* (1986) proposed a 'Zone of *Vascoceras tavense*' for beds at Pindiga and Ashaka making up the lower part of the Cauvini Zone as here defined. As Freund & Raab (1969: 23–24) pointed out, *V. tavense* Faraud (1940: 43; pl. 1, fig. 1; pl. 5, fig. 1; pl. 8, fig. 2) is a very poorly defined species. Berthou *et al.* (1985: pl. 3, figs 11, 12) refigured the corroded holotype photographically and showed its inadequacy as the basis of a new species. They remarked upon similarities with *Spathites* (*Jeanrogericeras*) Wiedmann, 1960 but regarded *V. tavense* as a *nomen dubium*. A Zone of *V. tavense* is not

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Figs 12–15 *Vascoceras cauvini* Chudeau. Figs 12–14, Pindiga Formation, Ashaka Quarry. Figs 12a, b, C.91272, × 1. Figs 13a, b, C.91271, × 1. Fig. 14, C.91274, × ⅔. Figs 15a, b, Pindiga Formation (Cauvini Zone), Pindiga. C.91278, × 1.

Figs 16–18 *Vascoceras* sp. juv. Fig. 16, Pindiga Formation (Cauvini Zone), Deba Habe. C.91256, × 1. Figs 17–18, Pindiga Formation (Cauvini Zone), Pindiga. Figs 17a, b, C.91263, × 1. Figs 18a, b, C.91264, × 1.

All specimens are housed in the British Museum (Natural History), London.

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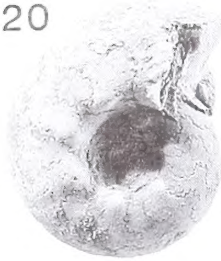

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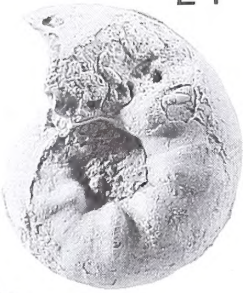

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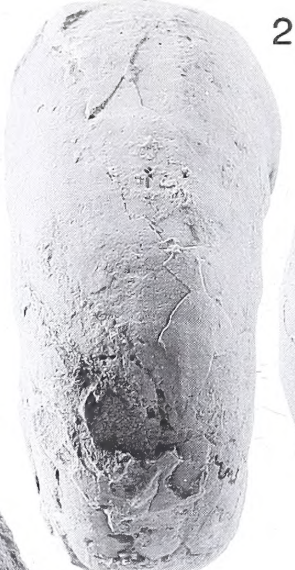

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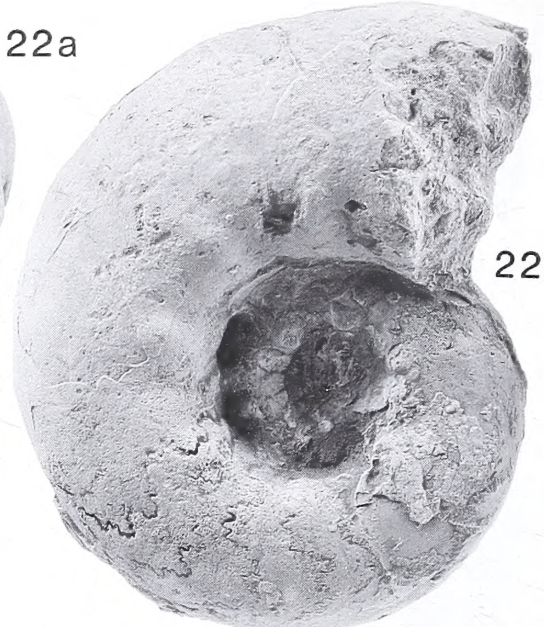

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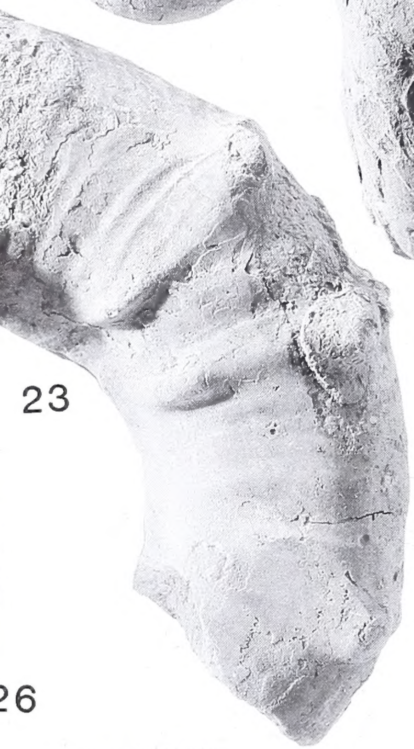

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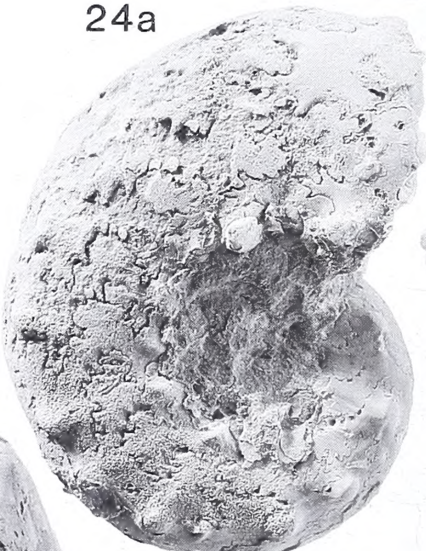

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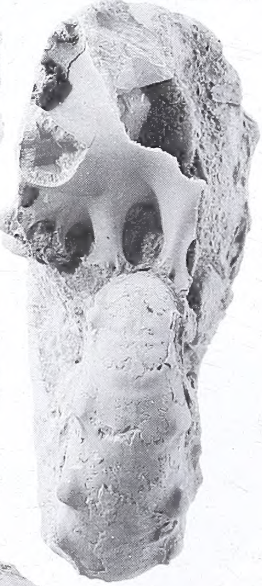

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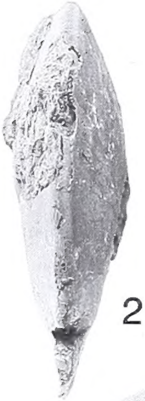

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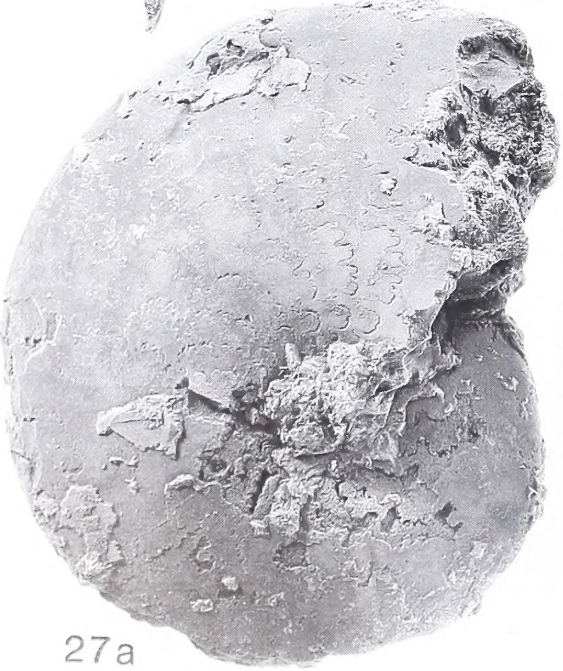

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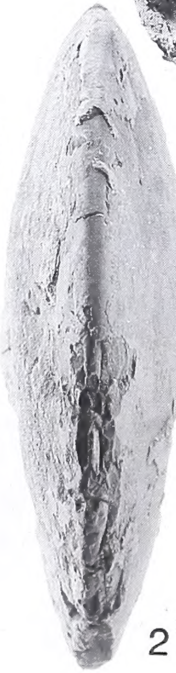

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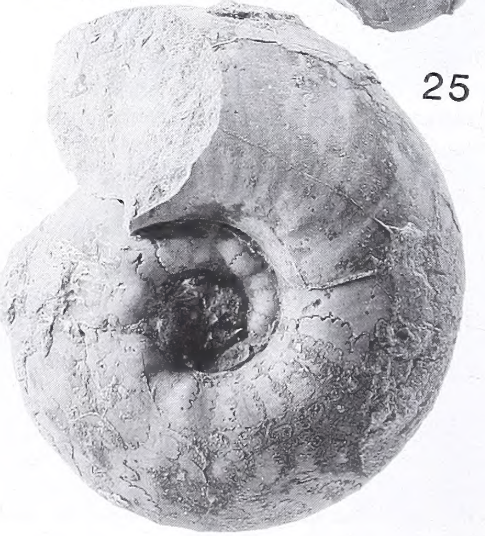

adopted here; all the *Vascoceras* occurring at these stratigraphical levels can be referred to *V. cauvini*.

The Cauvini Zone can be recognized at Pindiga, Ashaka and Deba Habe. The upper part is probably represented in the lower Dukul Formation at Dukul.

The *Vascoceras proprium* Zone

This zone encompasses the uppermost part of the *Vascoceras bulbosum* Zone and the *Paravascoceras costatum* Zone as applied by Barber (1957) and Popoff *et al.* (1986) (see Fig. 2). Its base is defined at the appearance of *V. proprium* which at Pindiga is the upper 'crystalline limestone' of Barber's (1957: table 3) unit 5. At Ashaka the base occurs at the bottom of unit 5 of Popoff *et al.* (1986: 348).

Paravascoceras costatum (Reyment 1954*a*: 257; pl. 3, fig. 6; pl. 4, fig. 3; pl. 5, fig. 2; text-figs 3a, b, 5), previously employed as a zonal index in north-eastern Nigeria, has recently been listed, along with *Pachyvascoceras* (=*Vascoceras*) *globosum* Reyment (1954*a*: 259; pl. 3, fig. 3; pl. 5, fig. 4; text-figs 3c, 7), as a synonym of *Vascoceras proprium* (Reyment 1954*a*: 258; pl. 5, figs 1a, b; text-figs 3d, 6) by Kennedy *et al.* (1987: 46). The Proprium Zone is condensed at Ashaka and in the region around Gulani and Bularaba (Fig. 1). It contains an enormous array of rather compressed to highly depressed *Vascoceras* in these areas, mainly referred to *V. globosum* and *Paravascoceras costatum* by Barber (1957). These faunas are in need of detailed revision but, in agreement with Kennedy *et al.* (1987), it has not proved possible to distinguish *P. costatum* as a discrete species. It is a variant of *V. proprium* with suppressed umbilical tuberculation but ventral ribbing in the adult stages. *V. cauvini* and *V. nigeriense* extend into the Proprium Zone, along with the juvenile *Vascoceras* mentioned above in connection with the upper part of the Cauvini Zone. *Thomasites gongilensis* appears in the Proprium Zone. The various forms referred to *Paramammites* Furon and *Nigericeras* Schneegans by Barber (1957) occur in the Proprium Zone. They are not, however, typical members of either of these genera. Similar material is common at Ashaka and shows an ornament characteristic of the Euomphaloceratinae Cooper, 1978 in the early and middle growth stages with seven rows of tubercles and much multiplied ventral ribbing. Unlike true *Paramammites* there are marked siphonal tubercles persisting to diameters as high as 70 mm. The suture lacks the square, bifid first lateral saddle typical of *Nigericeras* (Figs 19A–D), its elements being more elongate and the lateral lobe wider, while these forms show stronger and more persistent ornament. They often resemble *Nigericeras ogojaense* Reyment (1955: 62; pl. 13, fig. 6; pl. 14, fig. 3; text-fig. 28) and, to a lesser extent, *N. scotti* Cobban (1971: 18; pl. 9, figs 1–4; pl. 18, figs 1–9; text-figs 15–19). These species also show divergence from the type species, *N. gignouxi* Schneegans, 1943, in the characters mentioned above. Finally, Wozny & Kogbe (1983) reported *Metengonoceras dumbli* from their *Paravascoceras costatum* Zone (= Proprium Zone as employed here), although in the present study it has been found only in the Gadeni Zone.

The Proprium Zone can be recognized at Pindiga, Ashaka, Balbaya, Gulani and Bularaba (Fig. 1). Characteristic members of its fauna are present in surface scree at Deba Habe and Dukul. In the area between Balbaya and Bularaba it makes up the basal part of the limestone-bearing beds.

The *Pseudotissotia nigeriensis* Zone

As employed here, the *Pseudotissotia nigeriensis* Zone corresponds with that of Popoff *et al.* (1986), its base being marked by the appearance of *P. nigeriensis*. *Thomasites gongilensis* reaches its acme in the lower half of this zone where it may occur in very large numbers. Wozny & Kogbe (1983) proposed a 'Zone of *Gombeoceras gongilense*' for these horizons. As noted by Popoff *et al.* (1986), however, *Thomasites* [= *Gombeoceras*] *gongilensis* occurs both lower and higher and, following these authors, a separate zone is not distinguished here. At Pindiga and Ashaka the acme of *T. gongilensis* coincides with the occurrence of *Pseudaspidoceras* of *P. flexuosum* Powell, 1963 type (Figs 23, 24). *Vascoceras proprium* extends into the lower part of the Nigeriensis Zone, while *Neoptychites*, *Choffaticeras* and *Mammites*? occur as rarities. *Eotissotia simplex* Barber is common in its upper part. At several localities, notably Dukul, the more compressed and smoother varieties of *Pseudotissotia nigeriensis* occur higher in the zone, the earlier members resembling, indeed merging with, *Thomasites gongilensis*.

The Nigeriensis Zone can be recognized at Pindiga, Ashaka, Deba Habe, Dukul, Balbaya, Gulani and Bularaba.

The *Wrightoceras wallsi* Zone

A 'Zone of *Wrightoceras wallsi*' was first proposed for north-eastern Nigeria by Reyment (1965) but was intended to include the entire sequence from Gadeni to Wallsi Zone as employed here. Popoff *et al.* (1986) used the zone in a more restricted sense for beds including the upper part of the range of *Pseudotissotia nigeriensis*. Wherever the stratigraphical relationships have been seen (Pindiga, Ashaka, Deba Habe, Dukul and Bularaba), *W. wallsi* occurs only at these high levels. Apart from the index species, the Wallsi Zone contains *P. nigeriensis* and *Eotissotia simplex*, both of which are common.

Popoff *et al.* (1986) proposed a 'Zone of *Choffaticeras barjonae*' for the uppermost ammonite-bearing beds at Pindiga and a 'Zone of *Fagesia* n. sp. aff. *spheroidalis* Pervinquière' for those at Ashaka. These zones were correlated with one another even though, in fact, they contain no ammonites in common. A form similar to *Fagesia superstes* var. *spheroidalis* Pervinquière (1907: 324; pl. 20, figs 3a, b, 4, A) also occurs at Dukul (see below, Figs 32, 33) but in beds younger than those

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Figs 20, 21 *Vascoceras* sp. juv. Fig. 20, Pindiga Formation (Cauvini Zone), Pindiga. C.91262, × 1. Fig. 21, Pindiga Formation (Cauvini Zone), Deba Habe. C.91257, × 1.

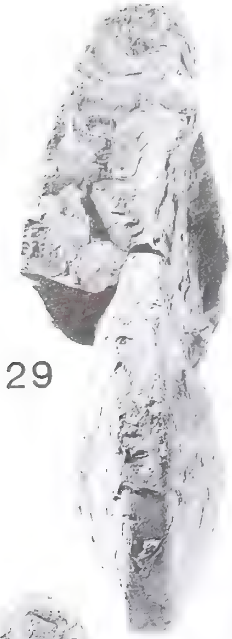
Figs 22a, b *Pseudaspidoceras* cf. *pseudonodosoides* (Choffat). Lower Dukul Formation, Dukul. C.91232, × 1.

Figs 23, 24 *Pseudaspidoceras* cf. *flexuosum* Powell. Fig. 23, Pindiga Formation (lower part of Nigeriensis Zone), Ashaka Quarry. C.91275, × ¾. Figs 24a, b, Pindiga Formation (lower part of Nigeriensis Zone), Pindiga, C.91276, × 1.

Fig. 25 *Vascoceras nigeriense* Woods. Pindiga Formation (Proprium Zone), Ashaka Quarry. C.91277, × ¾.

Figs 26, 27 *Hoplitoides ingens* (von Koenen). Upper Dukul Formation, Dukul. Fig. 26, C.91247, × 1. Figs 27a, b, C.91246, × 1.

All specimens are housed in the British Museum (Natural History), London.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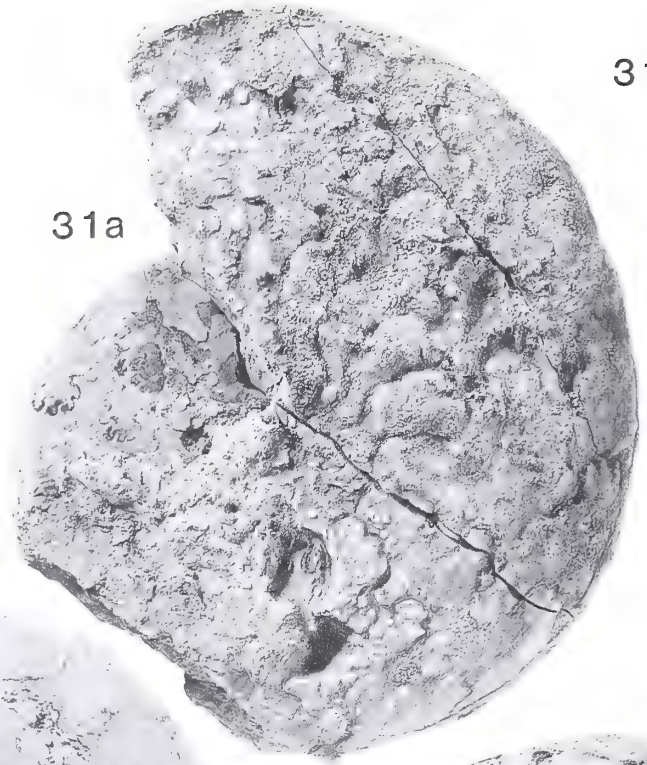
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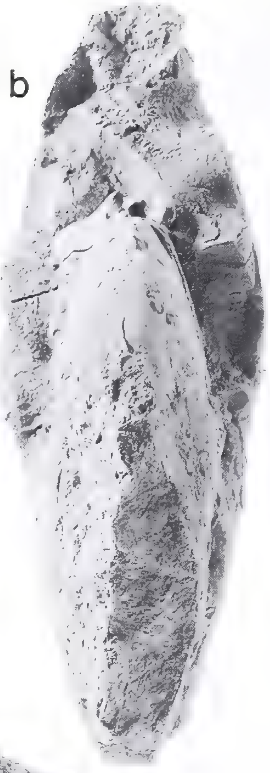
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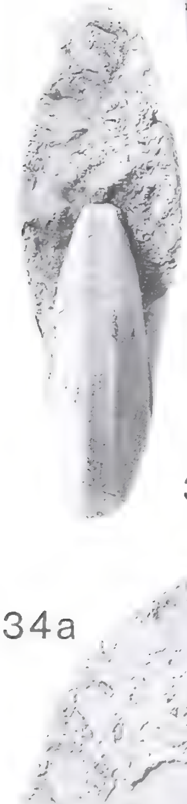
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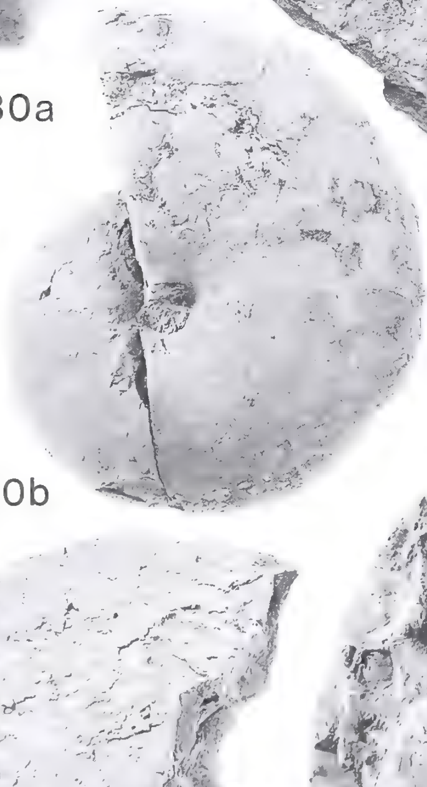
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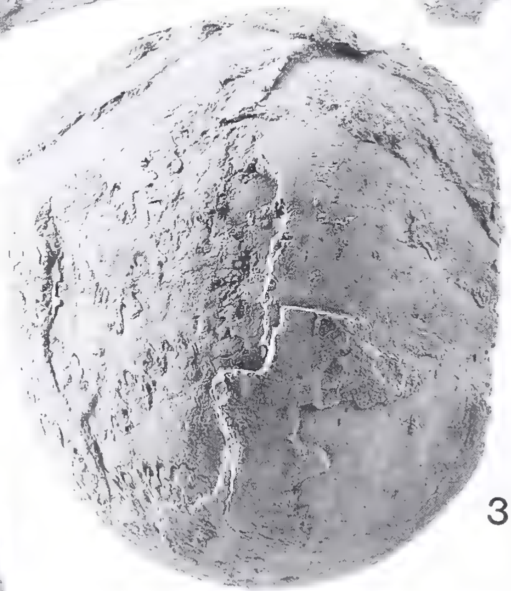
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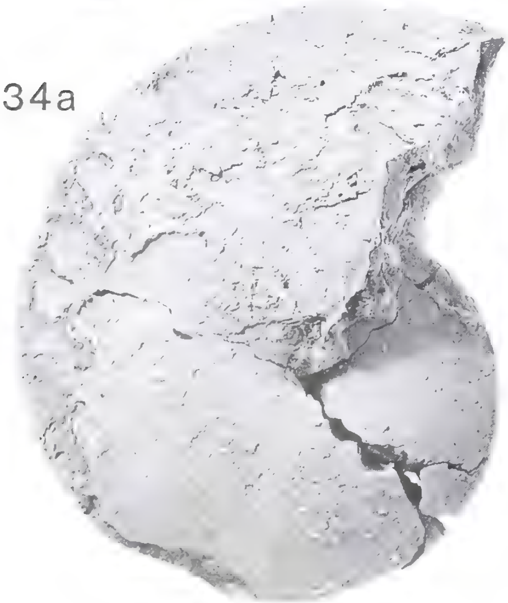
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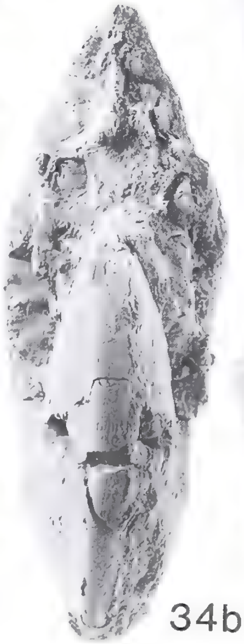
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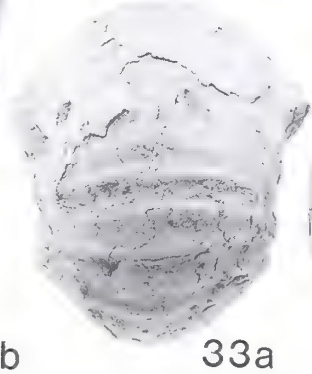
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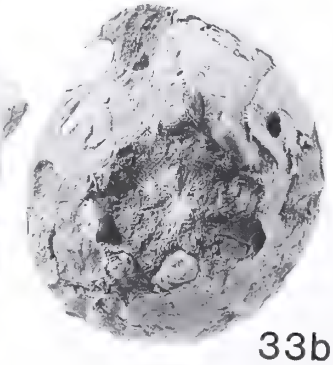
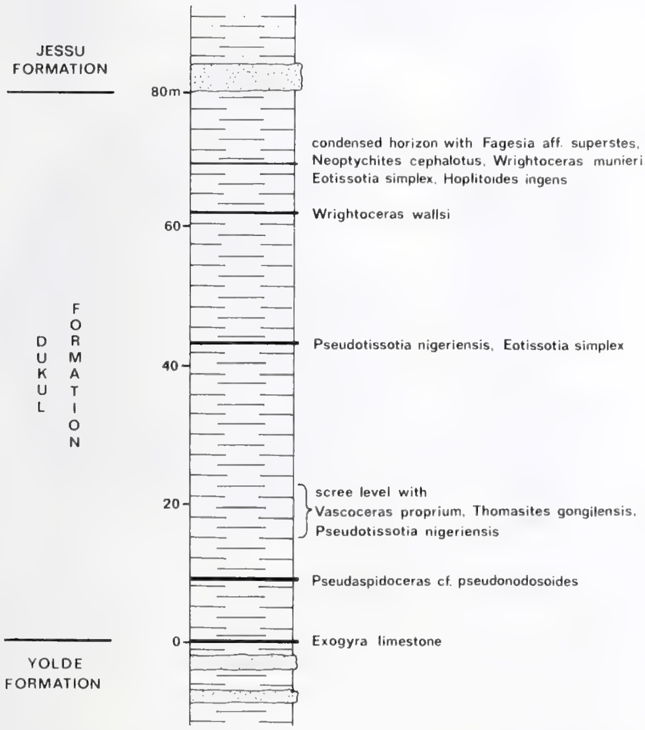

33b

at Ashaka. Nowhere else in the region have the index species of Popoff *et al.* been found. *Wrightoceras wallsi* persists throughout their Zone of *Fagesia* n. sp. at Ashaka. Their Barjonae Zone at Pindiga also contains species (*Eotissotia simplex* and *Thomasites gongilensis*) persisting from below. These two zones cannot yet be applied over north-eastern Nigeria as a whole and they are not differentiated here from the Wallsi Zone. It is, however, possible that in the future a discrete zone might be recognized at this stratigraphical level.

The Wallsi Zone outcrops at Pindiga, Ashaka, Deba Habe, Dukul and Bularaba. The index species has also been reported from Gulani and south-east of Numan (Barber 1957, Carter *et al.* 1963).


JESSU FORMATION
80m
60
40
20
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DUKUL FORMATION
YOLDE FORMATION
condensed horizon with Fagesia aff. superstes, Neoptychites cephalotus, Wrightoceras munieri, Eotissotia simplex, Hoplitoides ingens
Wrightoceras wallsi
Pseudotissotia nigeriensis, Eotissotia simplex
scree level with Vascoceras proprium, Thomasites gongilensis, Pseudotissotia nigeriensis
Pseudaspidoceras cf. pseudonodosoides
Exogyra limestone

Fig. 28 Stratigraphical section of the Dukul Formation at Dukul, showing the positions of the main limestone beds and their ammonite faunas.

Younger Turonian faunas

At its type locality, Dukul village (Fig. 1), the upper part of the Dukul Formation includes a 10-cm calcareous bed overlying the Wallsi Zone (Fig. 28). This bed contains phosphatic pebbles and laths, comminuted vertebrate remains and phosphatized gastropod moulds. Numerous ammonites also occur, with the exception of one specimen of *Fagesia*, all those recovered being wholly or partially phosphatized and some showing signs of reworking. The fauna includes rare *Eotissotia simplex* (Figs 19E, 37) and *Neoptychites cephalotus* (Courtiller) (Fig. 31) with more common *Wrightoceras munieri* (Pervinquière) (Figs 19M, 29, 30). Also present are scarce *Fagesia* (Figs 32, 33), similar to *F. superstes* (Kossmat 1897: 26; pl. 6, fig. 1) in the early whorls and later developing a highly globular shell shape like that in *F. superstes* var. *spheroidalis* Pervinquière. The Nigerian form, however, has peculiar, highly clavate umbilical tubercles, in places forming an almost continuous flange on the umbilical shoulder. The commonest ammonite in this fauna, though, is *Hoplitoides ingens* (von Koenen, 1897) (Figs 19F–K, 26, 27, 34). The timing of the transition from a truncated to an acute venter is variable in this material but all the variants are matched by specimens of *H. ingens* in a fauna from Wadatta in central Nigeria described by Reyment (1955: 79–81). Being highly condensed, no formal biostratigraphical unit is proposed for this bed; its fauna may eventually be found to span more than one biozone. It is, however, of great significance in allowing an upper age limit to be placed upon the Wallsi Zone (see below).

To the north of Bularaba (Bularafa) (Fig. 1) the Proprium to Wallsi Zones are present in the main limestone development of the Pindiga Formation. The immediately overlying strata are not exposed but some distance above the Wallsi Zone thin shelly limestones and calcareous sandstones occur containing *Coilopoceras discoideum* Barber, 1957 (Figs 19L, 35, 36) and *Placenticeras* aff. *cumminsi* Cragin, 1893 (Fig. 38). An assemblage zone characterized by these two ammonites is here proposed for these beds. *C. discoideum* is otherwise known only from the Mona region (Barber 1957, Grant 1965) some 150 km to the south (Fig. 1).

AGES AND CORRELATION

Correlation outside Nigeria

The Nigerian faunas discussed here are predominantly composed of members of the characteristically Tethyan family Vascoceratidae. Ammonite faunas of the Upper Cenomanian and Lower Turonian in north-west Europe, including the type areas, are, on the other hand, mainly Boreal in nature with the Mammitinae especially important. Problems of provinciality at these levels in the Cretaceous are well known. Sufficient data, however, are accumulating from various parts of the world to allow a reasonably reliable correlation with northern Nigeria.

The oldest ammonite-bearing beds in north-eastern Nigeria, the *Nigericeras gadeni* Zone, contain, west of Wajari, *Metoicoceras geslinianum*. These beds can therefore be firmly assigned to the Upper Cenomanian as previously suggested by Hancock & Kennedy (1981), Wozny & Kogbe (1983), Popoff *et al.* (1986) and Kennedy *et al.* (1987). They correlate with the *M. geslinianum* Zone of north-west Europe, now included in the Cenomanian (see, for example, Kennedy & Juignet 1973, Wright & Kennedy 1981, Hancock & Kennedy 1981). There are no ammonite faunas in north-eastern Nigeria of age equivalent to those with *Neolobites* Fischer which underlie beds of Geslinianum Zone age in many parts of the

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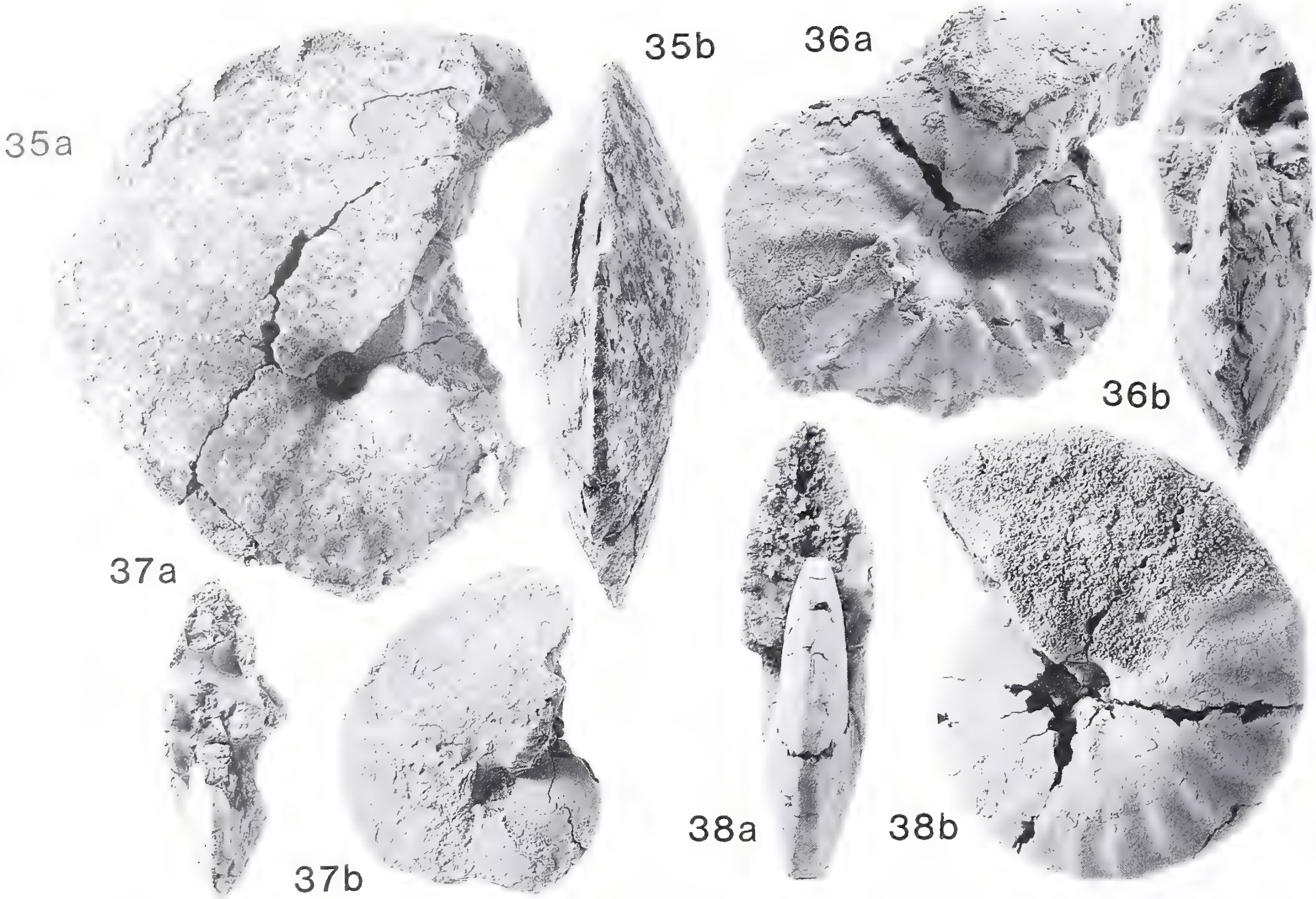
Figs 29, 30 *Wrightoceras munieri* (Pervinquière). Upper Dukul Formation, Dukul. Fig. 29, C.91236, × ¾. Figs 30a, b, C.91237, × 1.
Figs 31a, b *Neoptychites cephalotus* (Courtiller). Upper Dukul Formation, Dukul. C.91229, × ¾.
Figs 32, 33 *Fagesia* aff. *superstes* (Kossmat). Upper Dukul Formation, Dukul. Fig. 32, C.91231, × ¾. Figs 33a, b, C.91230, × 1.
Figs 34a, b *Hoplitoides ingens* (von Koenen). Upper Dukul Formation, Dukul. C.91245, × 1.
All specimens are housed in the British Museum (Natural History), London.



Figs 35, 36 *Coilopoceras discoideum* Barber. Pindiga Formation (Discoideum Zone), Bularaba. Figs 35a, b, C.91227, × ¾. Figs 36a, b, C.91226, × 1.
Figs 37a, b *Eotissotia simplex* Barber. Upper Dukul Formation, Dukul. C.91235, × 1.
Figs 38a, b *Placenticeras* aff. *cumminsi* Cragin. Pindiga Formation (Discoideum Zone), Bularaba. C.91233, × 1.
All specimens are housed in the British Museum (Natural History), London.

world, particularly Tethyan areas (see, for example, Greigert & Pougnet 1967, Freund & Raab 1969, Wiedmann 1960, Busson 1965, 1972, Kennedy & Juignet 1981, Amard *et al.* 1981, Berthou 1984).

The age of the *Pseudotissotia nigeriensis* and *Wrightoceras wallsi* Zones has been the subject of some disagreement. Barber (1957), Hancock & Kennedy (1981), Wozny & Kogbe (1983) and Kennedy *et al.* (1987) dated them Early Turonian, but Popoff *et al.* (1986) preferred a Middle Turonian age. The condensed horizon containing, amongst others, *Hoplitoides*, which occurs above the Wallsi Zone at Dukul, allows an upper age limit to be suggested for this zone. *Wrightoceras munieri* was used in Spain by Wiedmann (1960, 1979) and Wiedmann & Kauffman (1978) as an index species for the earliest Middle Turonian beds. Since *Mammites nodosoides* (Schlüter) is an associated species, however, Kennedy (1985) suggested that *W. munieri* should be assigned to the Lower Turonian in Spain. In Texas *W. munieri* occurs as low as the basal Turonian *Pseudaspidoceras flexuosum* Zone (Kennedy *et al.* 1987), while it is one of the first species to appear in the Venezuelan Turonian (Renz 1982). *Neoptychites cephalotus* is an early mid-Turonian species in the type area in France (Amédro *et al.* 1982, Robaszynski *et al.* 1983) but occurs in the lower part of the Lower Turonian in the western interior of the United States (Cobban & Scott 1972, Cobban 1984) and southern Nigeria (Zaborski 1987). *Fagesia superstes* also occurs in the Lower Turonian of the western interior (Cobban 1984) and Portugal (Berthou & Lauverjat 1979). *Eotissotia simplex* persists from the underlying Nigeriensis and Wallsi Zones at Dukul. Although *Hoplitoides latefundatus* Zaborski, 1987 occurs in the upper Lower Turonian of southern Nigeria, this genus is mainly of Middle Turonian age (Cobban & Hook 1980, Kennedy & Wright 1984). In the western interior of the United States it appears in the early Middle Turonian (Cobban 1984). In Nigeria *H. ingens* is thought to be characteristic of early Middle Turonian beds (Reyment 1978), the main occurrence of the genus being at Wadatta in the central part of the country.

This condensed fauna therefore contains elements which range from Lower to early Middle Turonian. Allix (1982) regarded the top of the Dukul Formation as basal Middle Turonian and an age very close to the Lower–Middle Turonian boundary is also suggested here. The Wallsi Zone below is almost certainly of late Early Turonian age, contrary to the opinion of Popoff *et al.* (1986). Further evidence to this effect is that *Choffaticeras barjonae*, proposed by these authors as the index species for a zone above limestones with *Wrightoceras wallsi* at Pindiga, occurs in beds assigned to the

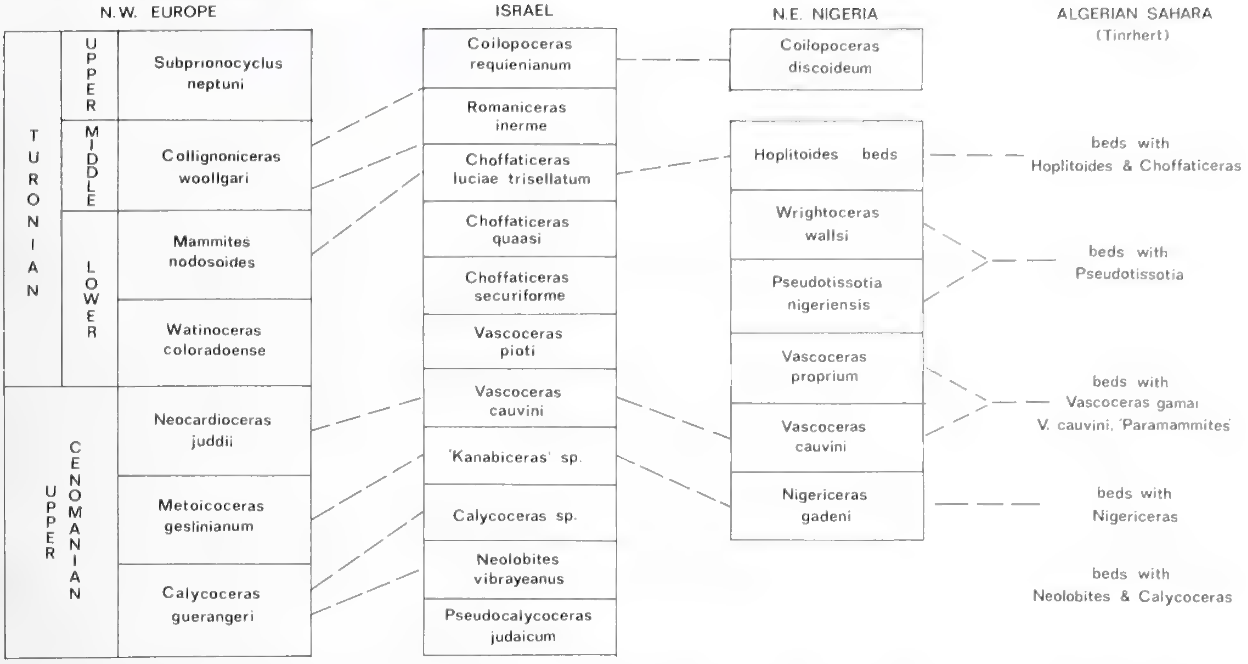

N.W. EUROPE
ISRAEL
N.E. NIGERIA
ALGERIAN SAHARA (Tinrhert)
TURONIAN
UPPER
MIDDLE
LOWER
UPPER
CENOMANIAN
Subprionocyclus neptuni
Collignoniceras woollgari
Mammites nodosoides
Watinoceras coloradoense
Neocardioceras juddii
Metoicoceras geslinianum
Calycoceras guerangeri
Coilopoceras requienianum
Romaniceras inerme
Choffaticeras luciae trisellatum
Choffaticeras quaasi
Choffaticeras securiforme
Vascoceras pioti
Vascoceras cauvini
'Kanabiceras' sp.
Calycoceras sp.
Neolobites vibrayeanus
Pseudocalycoceras judaicum
Coilopoceras discoideum
Hoplitoides beds
Wrightoceras wallsi
Pseudotissotia nigeriensis
Vascoceras proprium
Vascoceras cauvini
Nigericeras gadeni
beds with Hoplitoides & Choffaticeras
beds with Pseudotissotia
beds with Vascoceras gamai V. cauvini, 'Paramammites'
beds with Nigericeras
beds with Neolobites & Calycoceras

Fig. 39 Correlation of the Upper Cenomanian and Turonian in north-eastern Nigeria with the Algerian Sahara and Israel. Correlation between Israel and north-west Europe follows Lewy *et al.* (1984) and Kennedy (1985).

Lower Turonian in Portugal (Berthou 1984). Thus *Pseudotissotia* occurs considerably earlier in Nigeria than in France where the type species, *Ammonites galliennei* d'Orbigny, is of late Middle Turonian age (Kennedy *et al.* 1979, Amédro *et al.* 1982).

The Gadeni to Wallsi Zones in Nigeria therefore span an interval equivalent to the *Metoicoceras geslinianum* to *Mammites nodosoides* Zones in north-west Europe (Fig. 39). The chief remaining difficulty is the location of the Cenomanian–Turonian boundary. The Cauvini Zone in Nigeria is referrable to the Cenomanian. *Vascoceras cauvini* occurs in association with *M. geslinianum* over part of its range in Israel (Lewy *et al.* 1984). The latter species is known only from the Gadeni Zone in Nigeria, but, as noted previously, possible examples of *V. cauvini* are present in this zone. *V. cauvini* is an Upper Cenomanian species in the western interior of the United States (Cobban 1984). *Pseudaspidoceras pseudonodosoides*, common in the Cauvini Zone in Nigeria (see above, Popoff *et al.* 1986), occurs in the equivalent zone in Israel and in the uppermost Cenomanian *Neocardioceras juddii* (Barrois & Guerne) Zone of the western interior (Cobban 1984).

The overlying Proprium Zone contains, in its lower part, *Vascoceras cauvini* and *V. nigeriense*. The latter is very similar in its adult stages to *V. gamai* Choffat, 1898 (see Berthou *et al.* 1985 for a review), a species having its acme in the Upper Cenomanian. The Proprium Zone also contains the earliest examples of *Thomasites gongilensis*, a species which is known from the highest Cenomanian *Neocardioceras juddii* Zone and just below in southern England (Wright & Kennedy 1981) and in Brazil at a similar stratigraphical level (Bengtson 1983). Wozny & Kogbe (1983) also recorded *Metengonoceras dumbli*, a Cenomanian species (see Kennedy *et al.* 1981, Kennedy & Juignet 1984), from low in the Proprium Zone. In the lower part of the Nigeriensis Zone above, *Pseudaspidoceras* of *P. flexuosum* type occur at the level in which *Thomasites gongilensis* reaches its acme. The appearance of *P. flexuosum* is widely proposed as a marker for the base of the Turonian stage (Hancock 1984, Cobban 1984, Birkelund *et al.* 1984, Kennedy *et al.* 1987). As suggested by Hancock & Kennedy (1981) and Kennedy *et al.* (1987), the Cenomanian–Turonian boundary lies either within, or quite possibly at the top of, the Proprium Zone.

The stratigraphical position of *Coilopoceras discoideum* in Nigeria has previously seemed to be incongruous. It has, until now, been known only from the Mona region (Fig. 1), according to Barber (1957: 59), 'several hundred feet below the vascoceratid beds' (= Dukul Formation). This would imply a position well down in the Cenomanian. Grant (1965), on the other hand, believed it to be younger, occurring sometimes alone but in places with a typically early Turonian association of *Thomasites*, *Pseudotissotia*, *Vascoceras* and *Pseudaspidoceras*. He was, however, unable to recognize a detailed ammonite biostratigraphy. Both of these ages are at variance with current knowledge. Kennedy & Wright (1984) cast doubt on the reported occurrence of *Coilopoceras* in the Cenomanian of North Africa (see Pervinquière 1910). In the western interior of the United States the genus appears in the upper Middle Turonian but is mainly Late Turonian (Cobban & Hook 1980, Cobban 1984). In France its distribution is similar, from the *Romaniceras* (*R.*) *deverianum* (d'Orbigny) Zone (see Amédro *et al.* 1982), equivalent to the upper part of the *Collignoniceras woollgari* (Mantell) Zone of Kennedy *et al.* (1982) and Kennedy (1984) which these authors regarded as Middle Turonian, to the Upper Turonian *Subprionocyclus neptuni* (Geinitz) Zone. At Bularaba no continuous section is available but *Coilopoceras discoideum* certainly occurs some distance above the Wallsi Zone. Its only known associated ammonite is *Placenticeras* aff. *P. cumminsi*, a species found in the Lower and throughout the Middle Turonian of the western interior (Cobban 1984). At Bularaba there is no reason to believe that *Coilopoceras* appears unusually early and, as elsewhere, it can be assigned

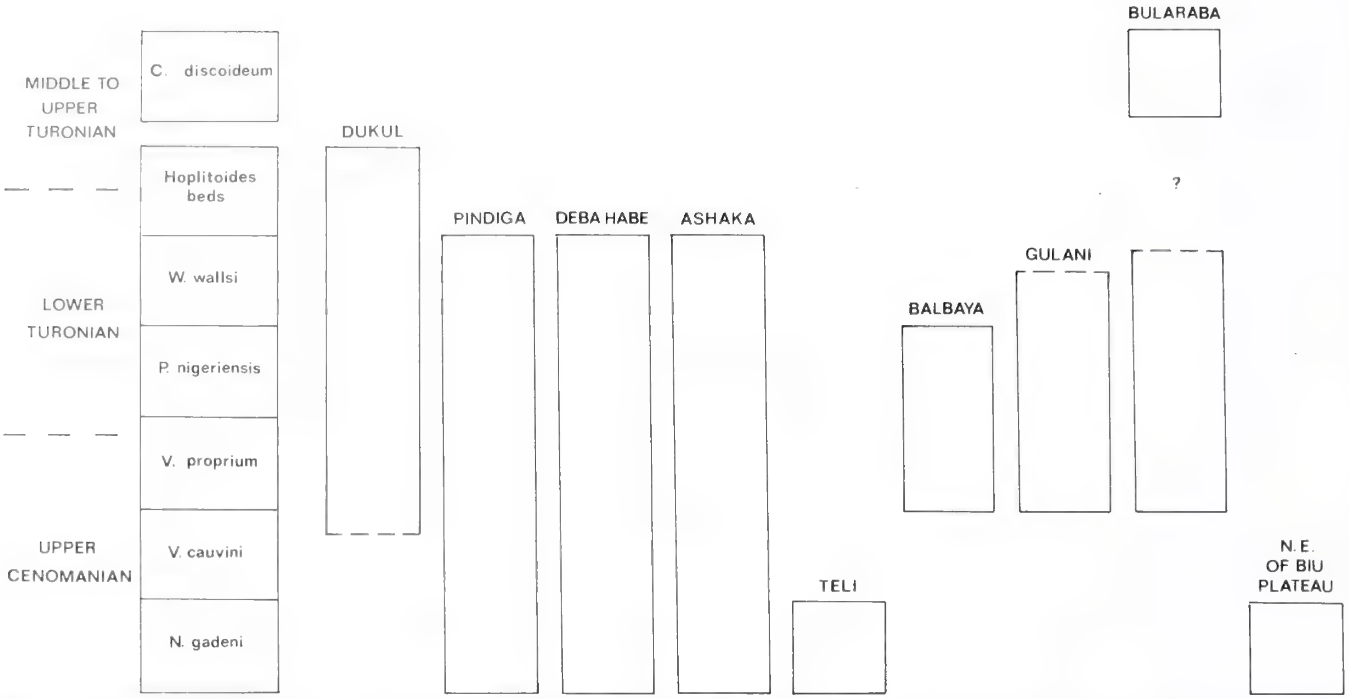


Fig. 40 Geographical distribution of ammonite biozones in north-eastern Nigeria. In most cases these biozones correspond with the limestone-bearing lithofacies.

to the upper Middle or Upper Turonian. Although the latter is more likely, a definite decision as to which is not possible in the current state of knowledge. As regards the occurrence of *C. discoideum* at Mona, it is significant that Lawal (1982) and Lawal & Moullade (1986) identified both Upper Turonian and Coniacian microfloras in the immediate area.

Whilst there are problems of provinciality involved in correlating the north-eastern Nigerian faunas with those of Boreal regions, comparison within the Tethyan province has been complicated by varying taxonomic opinions. The most straightforward correlation is probably with Israel (see Freund & Raab 1969, Lewy & Raab 1978, Lewy *et al.* 1984, and Fig. 39 herein for an ammonite biostratigraphy). There are no biostratigraphical equivalents in north-eastern Nigeria of the Israeli zones below that of '*Kanabiceras*' (properly *Euomphaloceras* Spath). The '*Kanabiceras*' Zone itself can be correlated with the Nigerian Gadeni Zone; both contain *Metoicoceras geslinianum* while *Nigericeras* of *N. gadeni* type (see Freund & Raab 1969: 19; pl. 2, fig. 1; text-fig. 40) occurs in the lower part of the Israeli zone. In the lower part of its range *Vascoceras cauvini* occurs alongside *M. geslinianum* in Israel and in Nigeria possible examples of *V. cauvini* are known from the Gadeni Zone at Pindiga. The *V. cauvini* zones in the two countries can also be correlated because of the occurrence of the index species and *Pseudaspidoceras* of *P. pseudonodosoides* type in both. The succeeding *Vascoceras pioti* (Peron & Fourtau), *Choffaticeras securiforme* (Eck) and *C. quaasi* (Peron) Zones in Israel cannot at present be directly correlated with Nigeria owing to a lack of common elements; there is only a record of *Pseudotissotia nigeriensis* from the Pioti Zone (Freund & Raab 1969: 50). The *Choffaticeras luciae trisellatum* Freund & Raab Zone in Israel, however, contains an assemblage including *Neoptychites cephalotus* and *Hoplitoides*, suggesting that it is broadly equivalent to the *Hoplitoides*-bearing bed at Dukul. The highest Turonian zone recognized in Israel is that of *Coilopoceras requienianum* (d'Orbigny) of late Middle or Late Turonian age; it can be regarded as broadly contemporaneous with the *C. discoideum* Zone in Nigeria. A noteworthy difference between the Lower Turonian of Israel and that of northern Nigeria, however, is the scarcity of *Choffaticeras* and corresponding abundance of *Pseudotissotia* and *Eotissotia* in the latter region. Interestingly, *Eotissotia simplex* is sometimes homoeomorphic with *Choffaticeras*; it may display a tricarinate venter in its middle growth stages and, more commonly, subdivision of most or all of the sutural saddles.

The Cenomanian–Turonian ammonite succession of the Algerian Sahara (see Busson 1965, 1972, Lefranc 1978, Amard *et al.* 1978, 1981; Fig. 39 here) is broadly similar to that in north-east Nigeria. There are, again, no Nigerian equivalents of the *Neolobites*-bearing beds in Algeria which include the upper parts of the ranges of *Calycoceras* Hyatt, *Eucalycoceras* Spath and *Pseudocalycoceras* Thomel and the lower part of the range of *Nigericeras* (Amard *et al.* 1978). The overlying beds in Algeria contain numerous *Nigericeras* without *Neolobites*, these horizons being equivalent to the earliest ammonite-bearing beds in northern Nigeria. The succeeding strata contain, amongst others, *Vascoceras cauvini*, *Paramammites laffittei* Collignon (1965: 186; pl. A, fig. 2) and *P. subtuberculatus* Collignon (1965: 187; pl. A, fig. 3), the last two being similar to and possibly conspecific with the various forms from Nigeria referred to *Paramammites* by Barber (1957). Next are beds with, in places, numerous *Pseudotissotia* (*Bauchioceras*) *nigeriensis* var. *egredians* Collignon (1965: 188; pl. H, fig. 1) and *P.* (*B.*) *bussoni* Collignon (1965: 190; pl. H, fig. 2), both, according to Hirano (1983), probable synonyms of *P. nigeriensis*. Collignon's figured specimens are especially close to microconchs of *P. nigeriensis* found at Deba Habe. In Algeria younger Turonian beds contain

Hoplitoides and, in the northern Tademaït region, *Coilopoceras* (Collignon & Lefranc 1974). Again *Choffaticeras* occurs in some numbers at these higher levels.

Correlation within Nigeria

In north-eastern Nigeria ammonites are almost exclusively confined to calcareous horizons and are therefore of biostratigraphical use only in formations containing such lithofacies. As shown in Fig. 40, the Cenomanian and Turonian limestones occur at various stratigraphical levels from place to place, as was pointed out by Lawal (1982) and Lawal & Moullade (1986). At Ashaka, Deba Habe and Pindiga limestone-bearing sequences ranging from the Gadeni to Wallsi Zone are present. At Dukul the Gadeni Zone has not been recognized. While the Dukul Formation includes an *Exogyra*-rich limestone at its base, the earliest ammonite present, *Pseudaspidoceras* cf. *pseudonodosoides*, occurs some 10 m higher in what is probably the upper part of the Cauvini Zone. The top of the Dukul Formation is a little younger than the highest ammonite-bearing beds at Pindiga, Deba Habe and Ashaka; no equivalent of the *Hoplitoides* fauna from Dukul is known at these localities. At Teli and north-east of the Biu plateau the Gadeni Zone alone is present. In the region between Balbaya and Bularaba the limestones of the Pindiga Formation belong to the Proprium Zone at their base. At Balbaya only ammonites typical of the overlying Nigeriensis Zone have otherwise been found but at Bularaba the main limestone body extends up into the Wallsi Zone. This species has also been reported from Gulani (Barber 1957), where the Nigeriensis Zone is also present. Apart from Mona, the Discoideum Zone is known only from Bularaba; but the strata intervening between it and the Wallsi Zone, and any ammonites they contain, are unknown.

Apart from varying in age, the limestone-bearing sequences differ markedly in thickness from place to place. In the Pindiga–Gombe–Deba Habe area variable, but consistently large, thicknesses are present. The Pindiga Formation here consists of a lower limestone-shale member and an upper shale member. The limestones, frequently marly, vary from a few cm to about 2 m in thickness. Their upper surfaces often mark minor sedimentary discontinuities. Around Pindiga village borehole records indicate thicknesses of 168 m, 294 m, and 330 m for the Pindiga Formation (Popoff *et al*. 1986). Estimates for the limestone-shale member vary: 60 m (Popoff *et al*. 1986), 80 m (Barber 1957), approximately 100 m (Wozny & Kogbe 1983). This last figure is probably closest to the true thickness. At Gombe town the limestone-shale member totalled about 65 m in one borehole (Thompson 1958, Carter *et al*. 1963: 49). To the south, at Kumo, the Pindiga Formation reaches nearly 800 m, the limestone-bearing part being in excess of 100 m in thickness (Lawal 1982, Lawal & Moullade 1986). At Deba Habe the limestone-shale member makes up the greater part of the Pindiga Formation, being about 100 m thick. At Dukul, the Dukul Formation is of comparable thickness, approximately 80 m, the formation again consisting mainly of shales, the limestones occurring as thin bands a few tens of cm in maximum thickness. At Ashaka the ammonite-bearing sequence is of intermediate thickness, approximately 20 m, the lower 9 m consisting mainly of massive limestones, the upper part shales with thinner interbedded limestones (see Wozny & Kogbe 1983, Popoff *et al*. 1986). North-east of the Biu plateau, on the other hand, the Gadeni Zone is represented by less than 1 m of hard, nodular limestone. The situation at Teli is comparable, though the Gadeni Zone may be slightly thicker. Between Balbaya and Bularaba the ammonite-bearing beds consist of condensed limestone sequences in which argillaceous and marly horizons are of subsidiary importance. At Balbaya the sequence is barely in excess of a couple of metres. It is rather thicker at Gulani and Bularaba but even here seems to be considerably less than 10 m, though no definite figures are available. In this region lithologies more closely resemble those at Ashaka than those in the Pindiga–Gombe area. Popoff *et al*. (1986: 357) found little purpose in separating the Gongila Formation and the overlying Fika Shale (see Carter *et al*. 1963) from the Pindiga Formation. This view is supported here, though Popoff *et al*. also suggested that the Dukul Formation might also be regarded as synonymous. This proposal is less tenable as the Upper Cretaceous sequence, at least in the eastern part of the Dadiya Syncline, is distinctive. In this region a sequence mainly comprising sands and silts (the Jessu Formation) separates the Dukul Formation from another major limestone-shale development of Coniacian age, the Sekule Formation (see Carter *et al*. 1963). Shales (the Numanha Shale) and sandstones (the Lamja Sandstone) complete the sequence, both being lateral equivalents of the Sekule Formation (see Petters 1978, Enu 1980, Allix 1982, Odebode 1987).

Clearly local subsidence history has had a profound effect on the lithological character and thickness of the Upper Cenomanian and Lower Turonian deposits in north-eastern Nigeria. During the Early Turonian the region between Balbaya and Bularaba seems to have been a relatively stable shelf area characterized by almost continuous limestone deposition. At Teli and north-east of the Biu plateau such conditions persisted for only a brief period during the Late Cenomanian. The Pindiga–Gombe–Deba Habe region, however, was characterized by strong subsidence virtually throughout Late Cenomanian and Early Turonian times, though the upper parts of the limestone beds here, sometimes rich in glauconite and containing reworked ammonites, often mark minor sedimentary discontinuities. Similar conditions prevailed to the south-east at Dukul where limestone deposition commenced a little later and persisted a little longer. At Ashaka limestone deposition characterized the Late Cenomanian but shales became the dominant lithology during the Early Turonian.

Allix & Popoff (1983) and Popoff *et al*. (1983) showed how, during the Early Cretaceous, sedimentation in north-eastern Nigeria was strongly influenced by faults, at first trending E–W and later NE–SW. Benkhelil (1982), Benkhelil & Robineau (1983) and Maurin *et al*. (1986) also stressed the importance of the latter structures, which they believed to be related to the South Atlantic transform fault system, during the Late Cretaceous. Sinistral strike-slip movement produced localized uplifted blocks and more extensive subsiding areas, 'pull-apart' or 'rhomb basins'. A number of such basins were identified by Maurin *et al*. (1986: fig. 12). Of these, the Pindiga and Lau Basins displayed the greatest rates of subsidence during the Late Cenomanian and Early Turonian.

Vascoceratid-dominated ammonite assemblages also occur in central and southern Nigeria. Particularly noteworthy are the Keana area with *Vascoceras nigeriense*, *V. proprium*, *Thomasites gongilensis*, *Pseudotissotia nigeriensis*, *Wrightoceras wallsi* and *Neoptychites* sp. (Offodile & Reyment 1976); and Ezillo with *Vascoceras*, *Fagesia*, *Thomasites gongilensis*, *T. koulabicus* (Kler), *Pseudotissotia nigeriensis*, *Wrightoceras* *wallsi* and *W.* cf. *munieri* (Zaborski 1987). Nowhere, however, is a detailed biostratigraphy available and the ammonite biozones applicable in the north-east cannot, as yet, be recognized outside that region. At Atom, near Makurdi, faunas including *Wrightoceras wallsi*, *Hoplitoides ingens*, *H. gibbosulus* (von Koenen) and *Mammites* spp. are present (Kogbe *et al.* 1978) but, again, the detailed stratigraphical relations of these forms are unclear. A little to the south, however, in the Icheri River near Igumale a fauna containing *Hoplitoides ingens* and *Neoptychites* (?)*cephalotus* overlies beds with *Wrightoceras wallsi* (Reyment 1955: 99), recalling the situation at Dukul. Furthermore, at Wadatta, immediately west of Makurdi, a diverse *Hoplitoides–Mammites–Benueites–Kamerunoceras* fauna (see Reyment 1955) is underlain by vascoceratid-bearing beds (Reyment 1978).

It should finally be noted that there is a marked change in both litho- and biofacies in the Lower Turonian around Lokpanta in southern Nigeria (see Zaborski 1987). Here black shales contain ammonites of boreal character. Basal Turonian beds characterized by *Watinoceras* spp. are overlain by a *Mammites nodosoides* Zone fauna containing *Hypophylloceras* sp., *Pachydesmoceras denisonianum* (Stoliczka), *Kamerunoceras puebloense* (Cobban & Scott), *Mammites nodosoides*, *Neoptychites cephalotus*, *Vascoceras venezolanum* Renz, *Paramammites polymorphus* (Pervinquière), *Fagesia catinus* (Mantell), *Hoplitoides latefundatus* Zaborski and *Herrickiceras*? sp. These black shales are, in the main, the age equivalents of the Nigeriensis and Wallsi Zones in the north-east of the country.

PALAEOBIOGEOGRAPHY

The palaeobiogeographical significance of the ammonite faunas of northern Nigeria has, in the past, often been difficult to assess as it had seemed that many of the forms present were endemic to the region. In opposition to the prevailing view (see Reyment 1980 for a review), Petters (1978) doubted that the northern Nigerian region was in direct connection with the trans-Saharan seaway during the Late Cretaceous. Popoff *et al.* (1986), however, showed that many of the Nigerian ammonite species are also known in the Saharan countries and elsewhere. Similarity is especially close in the Upper Cenomanian where *Metengonoceras*, *Nigericeras gadeni* and *Vascoceras cauvini* are important elements of the faunas in both north-eastern Nigeria and the Damergou area of Niger to the north (Chudeau 1909, Furon 1935, Schneegans 1943, Schöbel 1975). *Pseudotissotia nigeriensis* is also present at Damergou (Schneegans 1943), although in the Lower Turonian faunal similarity is reduced, *Thomasites*, *Eotissotia* and *Wrightoceras* being unknown there. *Pseudotissotia nigeriensis* is also present in the Algerian Sahara, as are *Nigericeras gadeni*, *Vascoceras cauvini* and forms probably conspecific with the Nigerian '*Paramammites*' of Barber (1957). The Late Cenomanian *Neolobites* faunas from the Saharan countries have no equivalent in Nigeria. Greigert (1966) showed that in west Africa they extend only as far south as southern Niger. Present evidence, therefore, indicates that vascoceratid ammonites first entered Nigeria from the north during *Metoicoceras geslinianum* Zone times. Microfossil evidence does indicate marine influence in the older Yolde Formation and, indeed, in the upper part of the Bima Sandstone (Doyle *et al.* 1982, Lawal 1982, Allix 1982) but environmental conditions seem to have been unsuitable for ammonites.

Marine microfossils are found virtually throughout the Upper Cretaceous in north-east Nigeria (Lawal 1982). Popoff *et al.* (1986) proposed that faunal exchange across the Sahara was continuous during the Late Cretaceous. The presence of *Hoplitoides* and *Coilopoceras* in north-east Nigeria indicates that marine conditions suitable for ammonites continued into the Middle and probably the Late Turonian here. Coniacian ammonites including *Forresteria* Reeside, *Barroisiceras* Grossouvre and *Tissotia* Douvillé occur in the limestones of the Sekule Formation in the Dadiya Syncline (see also Reyment 1954*a*, Barber 1960) and Santonian beds may exist a little further south (Reyment 1957). *Libycoceras* Hyatt has been found in Upper Campanian shales near Gombe (Reyment 1955, Zaborski 1982). Although, in ammonite terms, the major part of the Santonian and Campanian, and the whole Maastrichtian, are unknown, there is a growing body of evidence pointing to persistent marine conditions in north-eastern Nigeria during virtually the entire Late Cretaceous.

In southern and central Nigeria *Hoplitoides* is known in numbers from Wadatta and Igumale, while *Coilopoceras* (= *Glebosoceras* Reyment, 1954) occurs around Ogoja (Reyment 1954, 1957*a*) and north of Calabar (Zaborski 1985). *C. vandersluisi* Reyment (1957*a*: 62; pl. 10, figs 1a, b), indeed, is very similar to, and possibly synonymous with, *C. discoideum*. Kennedy & Wright (1984) suggested that *Glebosoceras globosum* Reyment (1954: 161; pl. 2, fig. 3; pl. 4, fig. 1; text-fig. 5) and *C. discoideum* may be a conspecific, dimorphic pair. Coniacian, Upper Campanian and Lower Maastrichtian ammonites are well known from southern Nigeria (Reyment 1954, 1954*a*, 1955, Zaborski 1982). Again, here it is Santonian to lower Upper Campanian forms that are unknown, although Klinger & Kennedy (1980: 110) speculated on the possibility of a Santonian age for *Reginaites quadrituberculatum* Reyment (1957*a*: 65; pl. 11, figs 1a, b) from near Agbani.

ADDITIONAL NOTE

After additional collecting at Ashaka, the following observations are relevant to the results of this paper and in particular to the position of the Cenomanian–Turonian boundary in north-eastern Nigeria. Firstly, weakly ribbed forms of *Thomasites gongilensis*, similar to those described from the Upper Cenomanian of Devon by Wright & Kennedy (1981), predominate in the Proprium Zone. Secondly, *Pseudaspidoceras* of *P. pseudonodosoides* type occurs in the Proprium Zone. And thirdly, *Pseudaspidoceras flexuosum* is present in the middle and upper parts of the Nigeriensis Zone (the species appears, however, at the base of this zone where large numbers of predominantly strongly ribbed *Thomasites gongilensis* occur). These further indications confirm the placement of the Cenomanian–Turonian boundary at or close to the top of the Proprium Zone, and the basal Turonian position of the Nigeriensis Zone.

Meister (1989) has recently published an extensive account of the Ashaka ammonites. It is not possible to make detailed comments on this work here but the following important points may be made concerning his proposed biozonation.

Meister's '*Nigericeras gadeni* Zone' corresponds not to that as proposed here, but to the Cauvini Zone. The forms he refers to *Nigericeras* are here regarded as *Vascoceras cauvini*. Such relatively compressed ammonites from this stratigraphical level at Ashaka, and elsewhere in north-eastern Nigeria, lack the typically acanthoceratid suture and seven rows of tubercles which characterize *Nigericeras*. True *Nigericeras* occurs below, in the Gadeni Zone as proposed here. This part of the sequence at Ashaka is not included in the section given by Meister (1989: fig. 41); its upper surface forms the floor of the quarry, but until 1987 it could be seen in vertical profile, but only in the eastern part of the quarry. It has subsequently been largely covered by dumping of overburden.

Meister (1989: 36) remarks on the astonishing diversity of morphotypes in the Proprium Zone and admits that he may have oversplit these faunas in his taxonomy. I think he does, and this explains the numerous biostratigraphical 'horizons' identified by Meister at the levels of the Proprium and lower Nigeriensis Zones as employed here.

Meister draws the base of his '*Pseudotissotia nigeriensis* Zone' at a higher level than that used here. The upper part of his '*Thomasites gongilensis* Subzone' is considered as part of the Nigeriensis Zone containing, as it does, the earliest, more tuberculated, forms of *P. nigeriensis*.

Meister employs *Wrightoceras wallsi* as a subzonal index with a further 'Subzone of *Fagesia superstes* or *Choffaticeras quaasi–C. pavillieri*' above. *Fagesia* of *F. superstes* type, however, extend higher than the ranges of either *W. wallsi* or *Pseudotissotia nigeriensis* at Dukul, while at Ashaka *Choffaticeras* appears not, as he suggests, at the level of his 'Superstes Zone' but considerably lower, in the middle part of the Nigeriensis Zone as proposed here.

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Two new amphisbaenians from the Lower Miocene of Kenya

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SYNOPSIS. Three partial skulls of two new species and genera (*Listromycter leakeyi* and *Lophocranion rusingense*) of Amphisbaenidae, from the Lower Miocene of Rusinga Island, Lake Victoria (Kenya), are described, illustrated, and compared with Recent amphisbaenians. *Listromycter leakeyi* is the largest amphisbaenian known. These new specimens extend the geographical range of the Amphisbaenidae into East–Central Africa, and they are the first fossil amphisbaenians of any age to be found in Africa.

INTRODUCTION

In 1947 the late Dr L. S. B. Leakey collected a quantity of vertebrate material from the Lower Miocene deposits on Rusinga Island, in the Kenyan waters of Lake Victoria. Three years later, in 1950, some of this material was sent to the British Museum (Natural History) in London; it included three small, very unusual skulls. All are broken and incomplete. The first, much the largest of the three, lacks the occiput and the lower jaw. The second and third lack the anterior portions and the lower jaw, each consisting of little more than the actual braincase. Yet there is just enough overlap between the first and the other two to indicate that the first is entirely distinct. The two smaller skulls, on the other hand, seem to be conspecific with each other.

The skulls were first recognized as amphisbaenian by the prominent median tooth in the first skull, the great solidity of the bones in relation to the size of the skulls, the lack of bony arcades, and the marked cranio-facial angle. However, more important as indicating that these animals could not be anything other than amphisbaenians were the extremely heavy premaxilla with its prominent facial process; the relatively few teeth and their relatively enormous size; the frontals completely surrounding the anterior end of the braincase; the peculiar interdigitating sutures between the elements comprising the braincase, resulting in a 'sandwich' construction of the latter; and, finally, the presence of a prominent processus ascendens of the supraoccipital fitting into a median notch behind the parietal. These characteristics and the general concordance between the architecture of the skulls and that of other amphisbaenians left no doubt that all three skulls had been properly assigned to that group.

The description of new genera of fossil amphisbaenians poses certain problems at present. Although the taxonomy of Recent species has now been reviewed (Broadley & Gans 1969, 1975, 1978*a*, *b*; Broadley, Gans & Visser 1976; Gans 1967*a*, *b*, 1971*a*, *b*, 1976, 1987; Gans & Alexander 1962; Gans & Broadley 1974; Gans & Kochva 1965; Gans & Kraklau 1989; Gans & Latifi 1971; Gans & Lehman 1973; Gans & Rhodes 1967), problems in the cranial osteology of the entire group have only recently been addressed (Bellairs & Gans 1983; Bellairs & Kamal 1980; Gans 1978; Jollie 1960). Numerous workers have illustrated amphisbaenian skulls (see Gans 1978 for references), but most of them have studied the same few species. Thus our knowledge of the skull in the species group *Monopeltis–Dalophia*, comprising 23 species, is based entirely upon four descriptions of *Monopeltis capensis* (Peters 1882; Zangerl 1944; Kritzinger 1946; Vanzolini 1951*a*). More extensive and detailed descriptions are being prepared.

Because of this the present paper can do little more than document the existence of the Kenyan material and describe it as fully as possible. We do include a brief discussion of the presumptive places of the new forms within the amphisbaenian radiation. Yet this analysis rests primarily upon the admittedly incomplete results of the generic review of the Amphisbaenia; it should therefore be regarded as preliminary.

ABBREVIATIONS

The following abbreviations are used in annotations of line drawings, Figs 2, 5 and 6.

bo	basioccipital
c_1	unidentified canal in premaxilla
c_2	unidentified canal in septomaxilla
ec	ectopterygoid
eo	exoccipital
f	frontal
fm	foramen magnum
f_o	foramen, presumably for the optic nerve
f_1	unidentified foramina in maxilla
f_2	
f_3	
f_4	unidentified foramen in posterolateral corner of nasal
f_5	unidentified foramen in anterior tip of vomer
f_6	unidentified foramen between palatine, pterygoid, maxilla and prefrontal
f_7	facial foramina for the VIIth nerve
g_1	unnamed groove extending forwards from the foramen for the Gasserian ganglion
m	maxilla
n	nasal
ocot	occipito-otic complex
op	opisthotic
os	orbitosphenoid
p	parietal
pbs	parabasisphenoid
pl	palatine
pls	pleurosphenoid
pm	premaxilla
pr	prootic
prf	prefrontal
pt	pterygoid
sm	septomaxilla
soc	supraoccipital
stp	stapes
v	vomer

SYSTEMATIC PALAEONTOLOGY

Suborder **AMPHISBAENIA** Gray, 1841
Family **AMPHISBAENIDAE** Gray, 1825

Genus ***LISTROMYCTER*** nov.

NAME. Greek λίστρον, spade, shovel; μυκτήρ, nose, snout. Refers to the spatulate rostrum, so well developed in the genus.

DIAGNOSIS. Large amphisbaenian with fairly short skull, dorsoventrally compressed snout and strong cranio-facial flexure; sutures well delineated; large median premaxilla with vertical process exposed in skull roof as long, broad bone extending forwards to form powerful spatulate rostrum and backwards to separate nasals entirely and frontals partly; nasal short, with concave anterior edge, extending not so far forwards as maxilla and premaxilla and thus producing embayment in dorsal view; external naris directed anteriorly, just below nasal embayment; premaxilla with one median tooth and three lateral teeth on each side; each maxilla with row of five teeth lying medial to line of premaxillary tooth row, and with stout stubby process directed anterolaterally from front end of its outer side; highly sinuous fronto-parietal suture; prefrontal partly outside and partly inside orbit; large braincase with marked sagittal crest; gap between parabasisphenoid and vomer, exposing orbitosphenoid in palatal view.

TYPE SPECIES. *Listromycter leakeyi* sp. nov.

Listromycter leakeyi sp. nov.

NAME. In honour of the collector, the late Dr L. S. B. Leakey.

DIAGNOSIS. As for the genus *Listromycter*, of which *L. leakeyi* is the only known species.

MATERIAL. Only the **holotype**, Nat. Hist. Mus. Palaeont. Dept. no. R.8292 (collector's field number 375A): skull lacking the occiput and lower jaw. Figs 1–2.

OCCURRENCE. Lower Miocene of Rusinga Island, Lake Victoria, Kenya.

Skull (general description)

The skull appears to have been larger than any other amphisbaenian skull known, fossil or Recent. It lacks the occiput and lower jaw; but the preserved portion, 29·5 mm long, extends backwards as far as a clean transverse break through the braincase (at the level of the middle of the pterygoids) and is reasonably complete. The upper surface and sides of the skull are in excellent condition, free of matrix and with well delineated sutures; most of the sutures and the surface sculpture may be distinguished without difficulty from the fracture lines, which are fairly abundant on some parts of the skull. The lower surface, on the other hand, was formerly obscured by a layer of soft buff-coloured sandstone, through which protruded the upper teeth. Careful treatment with dilute acetic acid has removed this sandstone and revealed a palate in as good a condition as the rest of the specimen. The interior of the braincase was cleaned in a similar manner.

The skull, as in all amphisbaenians, is divided into facial and cranial portions. This division is particularly marked on the dorsal surface, where the axis of the facial portion is bent down at an angle of about 50° to the axis of the cranial portion. The dorsal profile of the face, seen in lateral view, forms an absolutely straight line from the tip of the premaxilla to the fronto-parietal suture. From side to side, however, the upper surface of the face is smoothly convex, the rounding starting just above the lower margin of the skull. The ventral profile of the skull, like the dorsal profile, is bent down anteriorly at a point just behind the last tooth; the angle of the bend is rather less (about 30°).

A striking feature of the skull is the unusually large, thickened and spatulate rostral process; its magnitude is emphasized by the relative shortness, posterior position and concave anterior margin of the roof of the narial passage. The lateral limit of the facial portion of the skull is formed by the maxilla. A process projected anterolaterally just lateral to the narial passage, but now only a stump of this remains.

The orbit is not deeply recessed; the posterolateral wall of the facial region forms its anterior margin, the palato-pterygoid shelf forms its floor, and it is open behind. The posterolateral edges of the facial shelf converge backwards; they unite to form a marked sagittal crest which runs along the top of the cranial portion of the skull as far as the posterior break. The braincase is helmet-shaped in transverse section and has extraordinarily thick walls; it rests upon the posterior part of the palate (see below). The premaxillary rostral process projects well forward of the most anterior tooth.

The palatal surface is bounded by a smoothly rounded edge which forms an elliptical arc lateral and anterior to the tooth rows. The dentigerous surface of each maxilla extends medially past the tooth positions and projects like a shelf beneath the side of a wide, high central vault, roofed by the vomers and the palatines; it may be presumed that in the living animal the shelves on either side were united by a continuous floor of soft tissue, enclosing the internal choanal canals. The palatal shelf continues posteriorly beneath the orbit. Here its medial edge twists dorsally so that the shelf inclines at about 30° to the horizontal with its ventral surface facing obliquely inwards and downwards.

The cranial cavity is slightly wider than high at the site of the break; the flexure between the cranial and facial portions of the skull is also apparent within it. The cavity's diameter is least in the region of the anterior limit of the parietal. Immediately anterior to this there is a slight dorsal outpocketing just beneath the external boss which lies where the posterolateral edges of the facial shelf unite to form the sagittal crest. Farther forward still the cranial cavity increases in diameter again, though its axis now runs parallel to the face.

The skull is extremely solidly constructed. Not only are the individual bones fairly heavy, but they also show complexly interlocking sutures. The location of sutures, especially of those within the braincase, cannot be predicted from their appearance on the external surface of the skull. Elements do not meet in butt joints, but instead overlie each other in a complex manner. A lamina projecting from the edge of one element is often grasped between a pair of laminae from the adjoining one; this produces a very rigid 'sandwich' joint.

Dimensions

Length of facial plane: 23 mm. Length of cranial plane (as preserved): rather more than 10 mm. Estimated length of whole skull, measured in a straight line from tip of premaxillary rostral process to occipital condyle: about 36 mm.

Premaxilla (pm)

The unpaired premaxilla is enormous (length 12·7 mm). It consists essentially of a V-shaped tooth-bearing shelf; from the dorsal surface of this shelf rises a large, heavy vertical plate, expanded above into a transverse plate which is extended forwards to form the rostral process and backwards to form a broad complex exposure on the face.

The exposure on the facial plane consists of a more or less rectangular plate between the nasals, produced forwards into the rounded spatulate rostral process (slightly wider than the body of the bone) and produced backwards as an elliptical process which separates the frontals for half their length and is connected to the rest of the bone by an isthmus.

In lateral view the snout is sharply pointed, the angle between the facial plane and the dentigerous ventral surface being approximately 25°. Near and just dorsal to the most anterior tip of the maxilla, the premaxilla is perforated by a round, longitudinally running canal (c_1) which is open farther on the left than on the right side.

The anterior margin of the tooth-bearing portion forms a smoothly rounded but rather shallow rim (continued on either side for the whole length of the maxilla as far back as the orbit). The ventral surface of the premaxilla bears seven teeth arranged in the form of a V – one median tooth at the front, and two rows, each of three teeth, diverging backwards at an angle of 45° to each other. Only the last two teeth on the right side are preserved complete, the others being represented only by their broken bases. The elliptical median

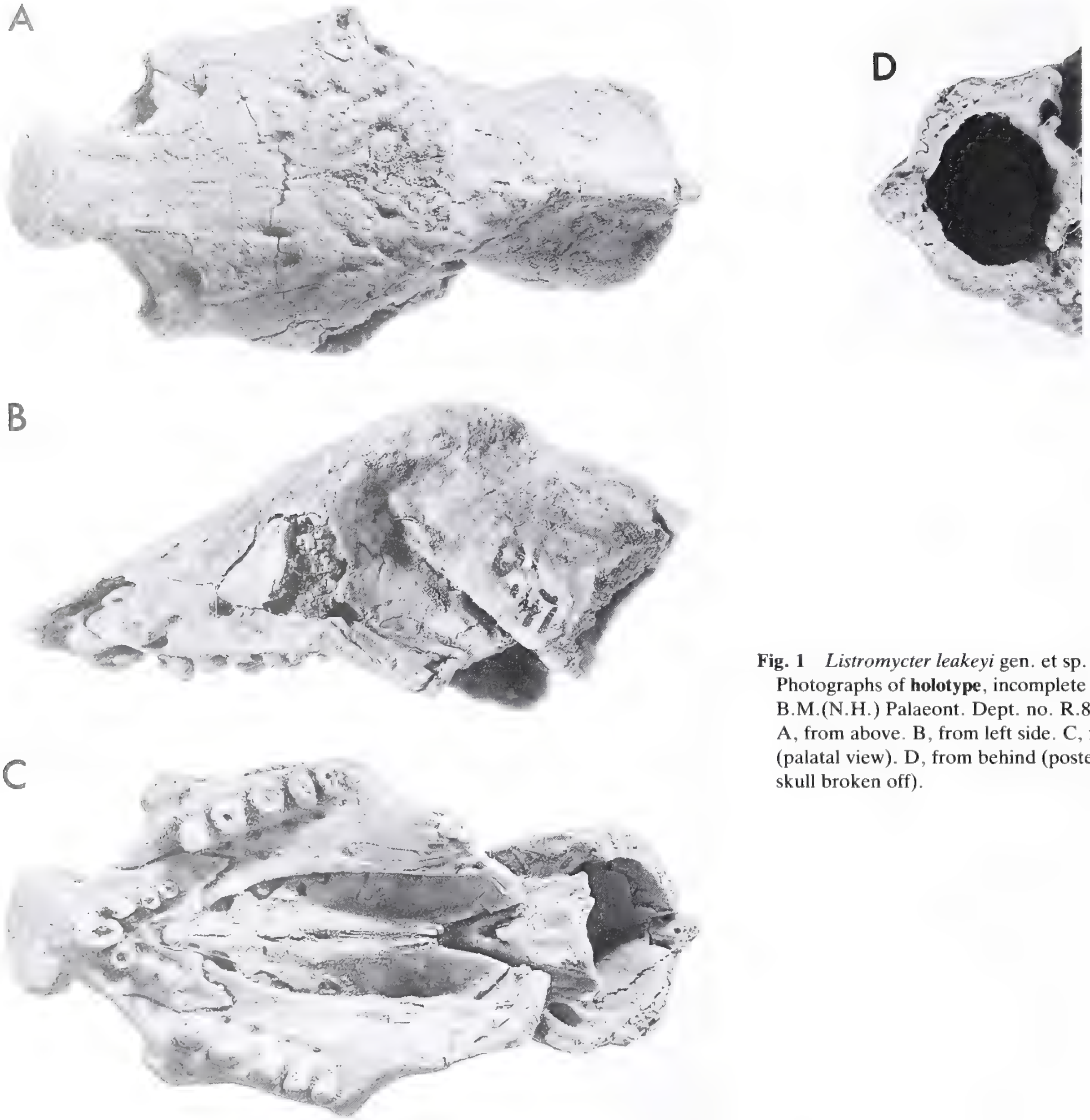
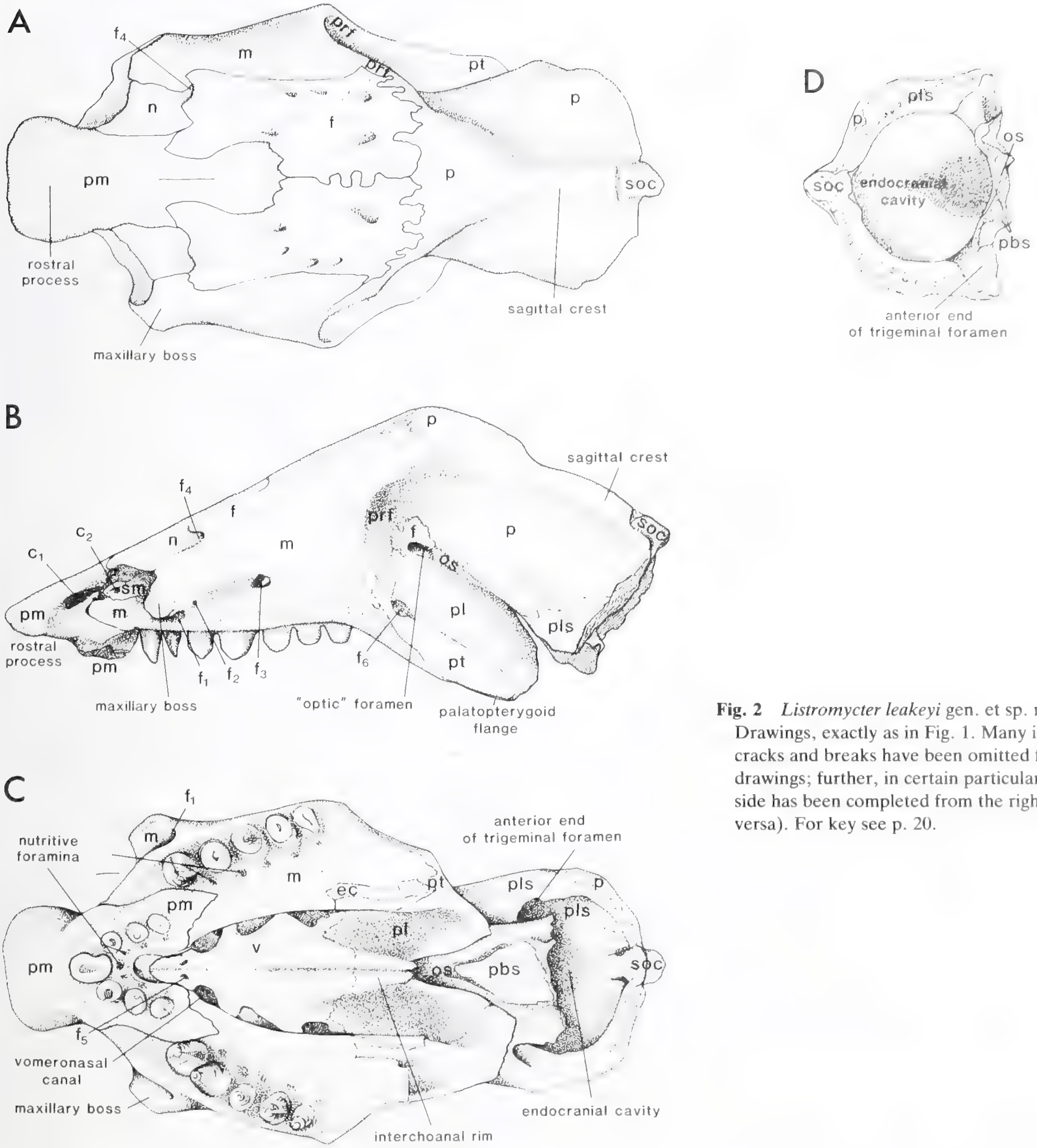


Fig. 1 *Listromycter leakeyi* gen. et sp. nov. Photographs of **holotype**, incomplete skull, B.M.(N.H.) Palaeont. Dept. no. R.8292, × 3·2. A, from above. B, from left side. C, from below (palatal view). D, from behind (posterior part of skull broken off).

tooth is by far the largest, the long diameter of the base being about twice that of the first lateral tooth. The second and third teeth are smaller still. All lateral teeth are circular rather than elliptical in section. The gap between the first and second lateral teeth is wider than the other gaps. All these teeth seem to be straight, bluntish cones with a central cavity. They are solidly anchylosed to a flat portion of the ventral surface; the method of attachment appears to be at least as much acrodont as pleurodont. A nutritive foramen lies immediately posterior to the medial side of the base of each tooth.

Maxilla (m)

The maxilla is a very heavy bone. It forms: (a) the palatal dentigerous shelf, (b) the floor, lateral wall, and part of the roof of the nasal passage (internal choanal canal), (c) a large part of the side of the face, up to the frontal suture above and the anterior rim of the orbit behind, (d) part of the palato-pterygoid shelf, and (e) a boss projecting anterolaterally. The size and importance of the maxilla may be gauged by the number (9) and the extent of its articulations with other elements, namely the premaxilla, the septomaxilla, the nasal, the frontal, the prefrontal, the pterygoid, the ectopterygoid, the palatine and the vomer.


A
f4
m
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prf
pt
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f
p
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p
soc
rostral process
sagittal crest
maxillary boss
D
p
pls
os
soc
endocranial cavity
pbs
anterior end of trigeminal foramen
B
p
sagittal crest
f4
f
c2
c1
n
m
prf
f
p
os
sm
pm
m
pl
pls
rostral process
pm
f1
f2
f3
f6
pt
maxillary boss
"optic" foramen
palatopterygoid flange
C
f1
m
nutritive foramina
m
anterior end of trigeminal foramen
ec
pt
pls
p
pm
pls
v
pl
pm
os
pbs
soc
f5
vomeronasal canal
maxillary boss
endocranial cavity
interchoanal rim

Fig. 2 *Listromycter leakeyi* gen. et sp. nov. Drawings, exactly as in Fig. 1. Many irrelevant cracks and breaks have been omitted from these drawings; further, in certain particulars, the left side has been completed from the right (and vice versa). For key see p. 20.

The curved anterior rim of the toothplate, mentioned above with reference to the premaxilla, is continued backwards by the maxilla.

In lateral aspect the maxilla has a roughly triangular appearance, the narrow apex of the triangle being directed forwards. This apex lies immediately beneath the external naris and projects into the premaxilla. Lateral to the naris lies the base of the maxillary boss; ventral to this stump is a horizontally elongate foramen (f_1) and, on the left side only, a smaller foramen (f_2) is present just posterodorsal to the first one. Yet another, even larger, foramen (f_3) may be seen dorsal to the gap between the second and third maxillary teeth, some way behind the boss. The posterodorsal horn of the triangle which the maxilla shows in this aspect just fails to reach the parietal, the two being separated by a narrow frontal–prefrontal connexion. The posteroventral horn extends down the lateral margin of the palato-pterygoid shelf to underlie the pterygoid in an oblique suture.

In palatal view the maxilla may be seen to bear a row of five teeth just medial to the rim. The line of these teeth does not continue the line of the premaxillary tooth row but, though parallel to that row, lies well outside it. Medial to the teeth the bone forms a prominent palatal shelf which projects ventral to the internal naris and the vaulted palate; anteriorly the shelf flares inwards to lie dorsal to the maxillary process of the premaxilla and to contact its median dorsal process. Another inward projection of the maxilla lies dorsal to the internal naris and palatal shelf and ventral to the lateral margins of the vomer. The broken posterior edge of the maxillary shelf shows a number of finger-like longitudinal depressions; in one of these lies the slender and elongate ectopterygoid which, anteriorly, almost reaches the last maxillary tooth. The remaining depressions contact what appear to be portions of the pterygoid, though the breaks are very irregular and the element concerned cannot be identified with certainty.

As stated above, five teeth are placed against the marginal rim of each maxilla. The second tooth is the largest, with the first, third, fourth and fifth in descending order of size. The cusps of all except the first left and last right tooth are broken at various levels. The spaces between the teeth are more or less equal. The teeth are elliptical in outline near their bases and are firmly fused to the maxilla in subpleurodont fashion (Gans 1957). The long axes of the ellipses are directed posteromedially. Shallow nutritive foramina lie medial and slightly posterior to the teeth at the point where the extension of the long tooth axis crosses the shallow lingual groove.

Nasal (n)
Each flatly oval nostril is roofed by a small nasal; its anterior edge forms a gentle concave curve. [After the writing of this description an attempt was made to remove more matrix from the cavity of the right external naris. Unfortunately this resulted in damage to the anterior edge of the nasal on that side. We both affirm, however, that this edge was previously a smooth concave curve, complete and apparently natural, as is confirmed by photographs and by the condition on the other side.] The dorsal exposure is roughly quadrilateral, small because the nasal is overlapped by the three adjacent bones. The posterolateral corner of the nasal is depressed into a foramen (f_4) that passes horizontally beneath the anterior process of the frontal and the wall of which also includes a small portion of the maxilla. Erosion of the nasals does not seem to be responsible for the peculiar shovel-shaped appearance of the snout. Certainly the survival of the delicate rostral tips of the septomaxillae argues for a minimum of erosion in this area and suggests that the embayment is natural.

Septomaxilla (sm)
The medioventral wall of the cavity of each external naris is formed by the shell-like septomaxilla, applied to the surfaces of the premaxilla above and the maxilla below. The slender anterior tip projects just beyond the front edge of the nasal; a little behind this tip is the aperture for a canal (c_2) which runs longitudinally back into the bone. The posterior part of the septomaxilla is still encased in the matrix filling the back of the nostril.

Vomer (v)
The vomers lie next to each other along the midline of the palate. Each has a slender anterior projection adjacent to the midline and a blunter posterior projection, and laterally each extends into a flat horizontal plate. The median edges of the vomers appear not simply to end in two straight edges abutting against each other, but to curve sharply dorsad into two parallel plates of unknown extent. In ventral exposure the vomers occupy an arrow-shaped area between the medial edges of the maxillae. The anterior tips lie ventral to the premaxilla, fitting into a median depression on the underside of that bone and extending as far forwards as the front of the last premaxillary tooth; each tip is perforated by a small foramen (f_5). The lateral edge of each vomer passes directly backwards, turns in towards the midline, and then, at the level of the second maxillary tooth, curves sharply outwards and disappears dorsal to the maxilla; the oval aperture left between the vomer and the maxilla at this point is the opening of the vomeronasal canal (Jacobson's organ). Posterior to this point the roof of the internal choanal canal is formed by the lateral portions of the vomers and, farther back, by the palatines. The lateral edge of the vomer appears once more, however, the bone being embayed to accommodate the supporting process which runs from the medial lamina of the maxilla to the palatal shelf. The straight, slender posterior projection that extends medial to the medial edge of the corresponding palatine forms the interchoanal rim.

Palatine (pl)
The palatine, as seen from below, is a semicylindrical bone forming the roof and sides of the choanal canal. Its lateral edge lies in close contact with, and dorsal to, the medial edge of the palato-pterygoid shelf. From here the bone curves outwards, first swinging laterad, then dorsad and mediad, and finally ventrad to complete the vault. The anterior portion of the medial edge of the palatine lies adjacent to the protruding posterior tip of the vomer and in fact forms the lateral portion of the posterior end of the interchoanal rim. The central portion of the bone is deeply concave. The anterior edge of the palatine lies ventral to the posterior edge of the vomer, projecting forwards so that the suture has a marked angulation of about 90°.

The palatine is broadly exposed in a lateral view of the skull, in which it may be seen to close the orbit ventrally. It extends dorsad from the pterygoid to articulate anteriorly in a complex series of sutures with the prefrontal and frontal, and dorsally with the orbitosphenoid. There is a deep foramen (f_6) close to the point of contact between the anterior tip of the palatine, the pterygoid, the maxilla and the prefrontal (clockwise in that order when viewed from the left).

Ectopterygoid (ec)
A slender rod-shaped ectopterygoid lies smoothly inserted in a furrow on the ventral surface of the posterior end of the maxilla. It extends into and possibly under the pterygoid. The anterior tip of the right ectopterygoid is broken off.

Pterygoid (pt)
The pterygoid forms the posterior portion of the palato-pterygoid shelf. Its anterior tip lies dorsal to the posterior part of the maxilla, with which it is in close and interdigitating contact. The shelf extends medially to the edge of the palatine vault, where both pterygoid and palatine are in contact with the base of the braincase.

Frontal (f)
The frontal is perhaps the most characteristically amphisbaenian element of the skull. Not only is there the usual extensive exposure on the dorsal surface of the skull (i.e. the 'face') and a minor exposure on the lateral wall of the orbit, but, with its fellow, the frontal forms also a complex and reinforced ring around the front part of the brain. It articulates complexly with the parietal and orbitosphenoid behind and

above and with the premaxilla, nasal, maxilla and prefrontal before and below. The following description is based on the external exposures of all these elements and also upon their internal exposures within the braincase.

The smoothly margined anterior wing of the frontal on the facial plane is separated from its fellow by the posterior process of the median premaxilla. The suture between the two frontals and the suture that they make with the parietal across the posterior apex of the 'face' are digitiform and interlock in a complex manner. The exposure of the frontal on the facial surface is markedly rugose; numerous foramina enter the bone, often from the end points of shallow canals.

Within the braincase the articulations of the frontal and the orbitosphenoid are again relatively simple. It may be seen by looking into the braincase from behind that the frontals form the roof, sides and floor of its anterior portion.

The exposure of the frontal on the anteromedial wall of the orbit is also complexly bent, and its margins show evidence of digitiform sutures with the palatine, the prefrontal and the parietal. A large foramen passes between the ventral margin of this exposure of the frontal and the orbitosphenoid; the foramen may be seen to run anteriorly and then curve medially.

Prefrontal (prf)
A short but relatively tall prefrontal forms the anterior wall of the orbit. It articulates laterally with the maxilla; dorsally with the facial exposures of the frontal and parietal; and medially with the parietal, the orbital exposure of the frontal and the palatine. Whether or not there was contact with the anterior tip of the pterygoid is not clear because of the broken condition of the specimen. All the sutures are digitiform.

Orbitosphenoid (os)
The amphisbaenian orbitosphenoid is a median bone that is apparently formed in membrane and may not be homologous with the element thus named in lizards (Bellairs & Gans 1983). It forms all that may be seen of the floor of the braincase in ventral view, except for the forwardly directed triangle in the midline which is the broken-off anterior part of the parabasisphenoid and underlies the orbitosphenoid; on either side lies part of the pleurosphenoid, also broken off behind. Anteriorly the orbitosphenoid is hidden by the palato-pterygoid flanges. It appears also in the lateral view of the skull between the lateral wall of the braincase (formed by the parietal) and the palato-pterygoid flange, extending forwards, between the parietal above and the palatine below, as far as the 'optic' foramen.

Within the braincase it may be seen that its floor is formed by the orbitosphenoid, immediately posterior to the ventral juncture of the two frontals and anterior to the tip of the basisphenoid. The bone is shortest in the ventral midline, where it appears to be faintly grooved as if composed of fused paired elements, though there is no suture line and the grooving appears to be restricted to the internal surface of the bone. The orbitosphenoid is produced anteriorly into a small, square-ended median process, which is clasped on either side by a small, backwardly projecting horn of the frontal. The anterior wings of the orbitosphenoid extend dorsad and anteriorly inwards to the fronto-parietal suture in the lateral wall of the braincase, overlapping that suture medially. Posteriorly the orbitosphenoid extends around the trigeminal foramen on either side, near the anterior edge of which the specimen is broken off. A single small foramen penetrates each side of the orbitosphenoid in the floor of the braincase.

Parabasisphenoid (pbs)
Only the anterior part of the parabasisphenoid is preserved. It appears as a narrow, forwardly directed triangle in the floor of the braincase, seemingly inserted into the back of the orbitosphenoid both internally and externally. In fact, however, the relations are more complex than they seem. The internal exposure obviously consists of a very thin sheet of bone fitting into a shallow, triangular depression on the upper surface of the orbitosphenoid. The external exposure consists mainly of a narrower, thicker, triangular sheet of bone projecting a little farther forwards and fitting into a correspondingly deeper depression, within which it has slipped back a little *post mortem* from its proper position; on either side of this median plate is a very much thinner lateral wing, projecting forwards but not so far. Just how far the orbitosphenoid extended back between these two sheets of parabasisphenoid, rather like the filling in a sandwich, is a matter for conjecture.

The inner suture seems to be radially digitiform on the right side but much straighter on the left; it is difficult to determine which is the natural condition. The cross section provided by the break through the skull indicates that the bone consists of a lamina forming the floor of the braincase, reinforced by a central thickening; the thickening bears three longitudinal external ridges below—a median ridge and, on either side, a lateral ridge which forms the margin of the central triangular plate. The thickened region corresponds to the centre of the interpterygoid vacuity.

Parietal (p)
The unpaired parietal forms much of the roof and sides of the braincase. It is shaped like a squat inverted trough, an inverted U; dorsally it is thickened by the sagittal crest, the anterior termination of which may be detected internally. The nature of the limits of the parietal and of its articulations with the frontals, prefrontals and orbitosphenoid has already been indicated in the appropriate sections above; the complex articulation with the pleurosphenoid and the contact with the supraoccipital are described immediately below.

Pleurosphenoid (laterosphenoid) (pls)
The pleurosphenoid (considered part of the prootic by Rieppel, 1981) appears on either side as a bone that forms a considerable part of the lateral wall of the braincase. Its union with the parietal is highly complex; the external and internal exposure patterns differ greatly, and once again it is obvious that in some places the elements overlap to a considerable extent. The external exposure of the pleurosphenoid on the preserved part of the skull is restricted to the posterolateral corner of the preserved portion of the braincase. Internally, however, the pleurosphenoid exposure extends up the wall of the braincase as far as the dorsal midline, where it makes contact with the supraoccipital. Thus, at the level of the fracture, the lower part of the lateral wall of the braincase consists entirely of pleurosphenoid, but in the upper two-thirds of the wall the thick pleurosphenoid is covered externally by the thin parietal. The cross section shows the pleurosphenoid itself to consist of two layers of dense bone with a central spongy layer and to be separated from the parietal by an undulating suture.

It may also be seen within the braincase that the parietal extends back towards the fracture line and overlaps the pleurosphenoid posteriorly. Thus it is evident that the pleurosphenoid extends farther forwards, hidden between two layers of parietal. On the dorsal side of the brain cavity the overlapping parietal is produced backwards into a pair of little horns, lying on either side of the supraoccipital and just reaching the level of the fracture posteriorly.

Supraoccipital (soc)
The hindmost tip of the preserved part of the sagittal crest is occupied by a separate bone, the anterior portion of the supraoccipital. Its suture with the parietal, as seen in the section of the skull afforded by the break, does not run straight through the thickness of the bone but forms an S-shape. Just anterior to the supraoccipital there is a wedge-shaped gap which may originally have been filled with cartilage, as in many Recent forms.

Phylogenetic position
Vanzolini (1951*b*) proposed a new subfamily of the family Amphisbaenidae, the Rhineurinae, characterized by a strong cranio-facial angle, a horizontally flattened face and a shovel-like snout. This classification was accepted in such standard works of reference as those of Hoffstetter (1955) and Romer (1956). Gans, however, suggested (1967*a*, 1974) that the various members of the 'Rhineurinae' had developed those same structural features in common because they all shared a style of burrowing called 'shovel-snouted digging' (Gans 1968, 1969) and that, in consequence, the assemblage was almost certainly polyphyletic. Berman (1973) raised the Rhineurinae to family status but separated some of Vanzolini's fossil rhineurines from North America into further distinct families. Gans (1978) accepted the Rhineuridae as a family but, unlike Berman, retained within it all the fossils from North America as well as the single Recent species from that continent; on the other hand, he left all the 'rhineurine' genera from other continents within the Amphisbaenidae.

Gans (1978) recognized also two other families: the Bipedidae (characterized by the retention of hypertrophied forelimbs and other derived characters) and the Trogonophidae (characterized by an acrodont dentition). No 'cladistic analysis' of the Lepidosauria as a whole had at that time been carried out. Gans' classification, however, was based upon a properly conducted character distribution analysis (essentially the same thing) of the genera concerned, and it is now supported further by the results of a wider, as yet unpublished generic/familial analysis.

Listromycter cannot be placed in the Trogonophidae, for its dentition is subpleurodont instead of acrodont. Its skull is very different in other respects; in particular, the cranial suture pattern of *Listromycter* does not accord with the oscillating style of locomotion peculiar to trogonophids. The new genus must therefore be compared with other 'shovel-snouted' extant amphisbaenians, of which there are four genera of Amphisbaenidae (*Monopeltis* and *Dalophia* from Africa; *Leposternon* and *Aulura* from South America) and one single species of the family Rhineuridae (*Rhineura floridana* from North America). *Monopeltis* has 16 species and *Dalophia* 7 (Broadley *et al.* 1976); the present range of neither genus comes closer than 500 km to Rusinga. *Leposternon* has approximately 7 species (Gans 1971*a*) and *Aulura* has but one (Gans 1971*b*).

Aulura is rare and its skull has never been described. The skull of *Dalophia* is also undescribed; in the points mentioned here, however, it is known to resemble that of *Monopeltis*. Indeed, there are only three Recent 'shovel-snouted' species of which the skull has been described: *Monopeltis capensis* from Africa (see p. 20), *Rhineura floridana* from North America (cf. Gans 1967*b*) and *Leposternon microcephalum* from South America (cf. Gans 1971*a*).

The adaptations for shovel-snouted digging in those three species may be arranged under four headings, the first two of which are to some degree related to each other and likewise the last two.

1. *Flattening of the skull.* In all three genera under discussion there is a very marked dorsoventral flattening of the skull, as contrasted with that of the generalized *Blanus* or *Amphisbaena* and even more with the 'spade-snouted' *Anopsibaena* (Gans & Kochva 1965). The dorsal surface, however, remains gently convex from side to side.
2. *Development of rostral shield.* In all three genera the anterior and lateral margins of the upper jaw are extended well beyond the tooth row so as to produce a wide, effective, digging (penetrating) spade with an arc-shaped cutting edge. This extension consists of outgrowths variously formed of the premaxilla and maxillae. A secondary result is the roofing over of the external nares which thus face downwards rather than anterolaterally; this protects them during both the penetrating and the tunnel-widening movements. Yet another effect of the shield development is that the skull appears even flatter than it otherwise would. (Again, contrast this with the conditions in *Blanus* and *Amphisbaena*.)
3. *Flexure of the skull.* The anterior portion of the skull is bent strongly downwards from a point on the cranial roof just behind the fronto-parietal suture. This produces a sharp angulation in the dorsal profile of the skull of between 45° and 70° and a somewhat lesser angulation in the ventral profile, and it results in the ventral deflection of the tooth row from the long axis of the body: in other amphisbaenians the anterior part of the skull is bent down through a much smaller angle (not more than 25°) and the flexure is a gentle curve rather than an abrupt angulation. A marked effect of this is to shorten the ventral perimeter of the skull between the rostral tip and the occipital condyle and, coincidentally, the length of the mandible (see also 4 below).
4. *Shortening of the skull.* In shovel-snouted digging a mechanical advantage is conferred by shortening the distance between the fulcrum and the point of force exertion (thus increasing the forces that may be exerted for whatever moment is generated by the musculature). This may explain the reduction, apparent in all three genera, in the relative length of the entire skull. Since any reduction of the occipital region must be limited by the spatial requirements of the braincase and of the auditory capsule, and since any reduction of the rostral region (the effective digging organ) is also disadvantageous, it is mainly in the anterior part of the cranial region that this shortening takes place.

The combined effect of adaptations 3 and 4 is to shorten the ventral surface of the skull to such an extent that the gap between the parabasisphenoid and the vomer closes entirely. In none of these three genera is the orbitosphenoid exposed in palatal view, and the tip of the cultriform process (the anterior rostrum of the parabasisphenoid) always fits between the posterior processes of the vomers.

Although *Listromycter* possesses all four of these adaptations, it is interesting to note that two of them (nos 2 & 4) are developed to a significantly lesser degree than in any of the three Recent genera:

1. The skull is flattened to much the same degree.

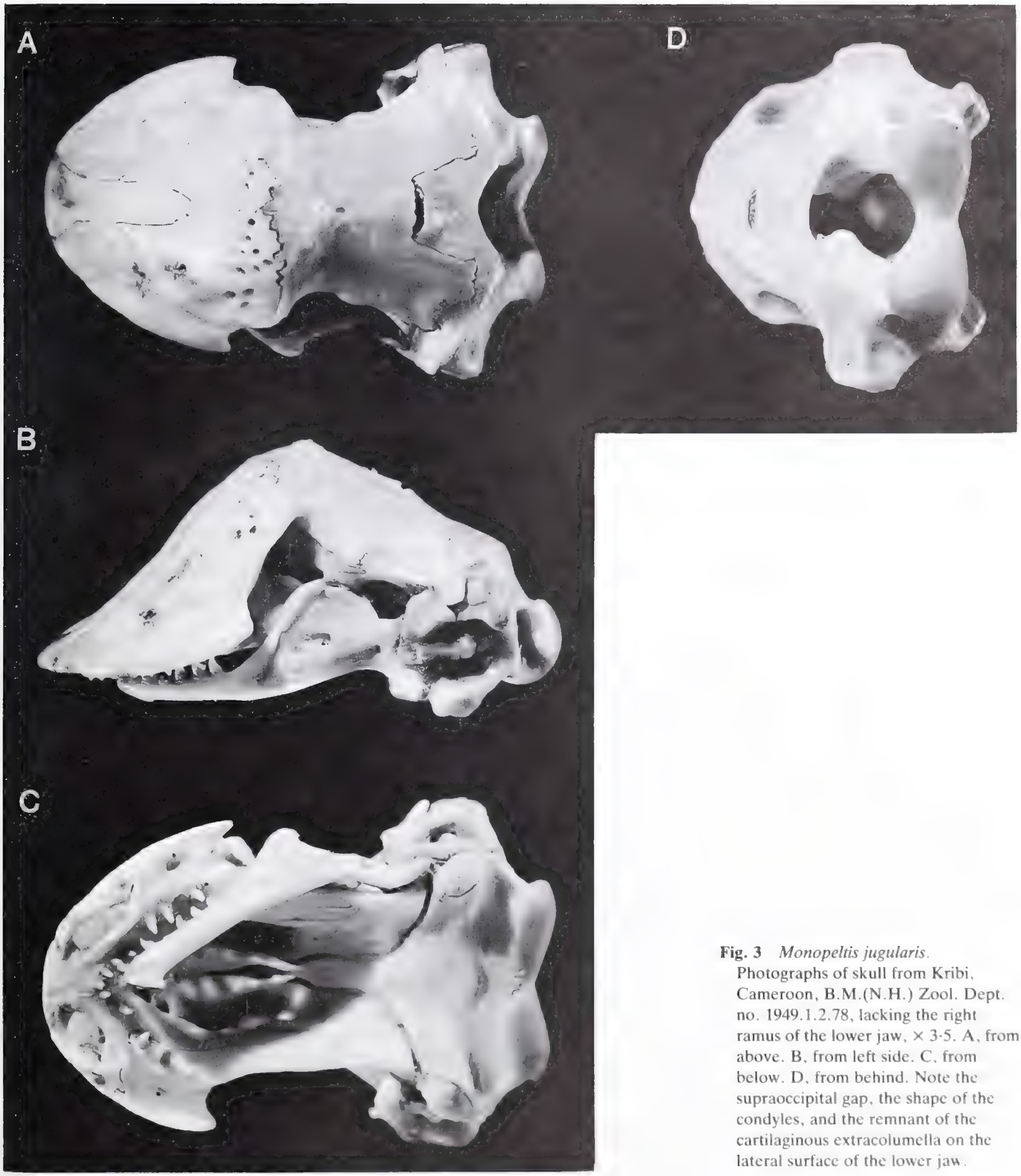


Fig. 3 *Monopeltis jugularis*. Photographs of skull from Kribi, Cameroon, B.M.(N.H.) Zool. Dept. no. 1949.1.2.78, lacking the right ramus of the lower jaw, × 3·5. A, from above. B, from left side. C, from below. D, from behind. Note the supraoccipital gap, the shape of the condyles, and the remnant of the cartilaginous extracolumella on the lateral surface of the lower jaw.

2. There is no complete bony rostral shield; but there is a very large anterior extension of the premaxilla, and each maxilla bears an anterolateral protuberance of unknown size (maxillary boss). On the other hand, the maxilla is not extended laterally beyond the tooth row as it is in *Monopeltis*. The external naris, in consequence, is not directed ventrally; it still faces anteriorly, a little dorsally and a little laterally, much as in *Blanus*. However, it is possible that the maxillary bosses in *Listromycter* were connected by a horny plate, which would have produced an arc-shaped cutting edge and a downwardly directed external naris much as in Recent forms.
3. There is a sharp cranio-facial flexure of the skull, measuring 50° in the dorsal profile. This is less than in *Monopeltis*

jugularis (70°), *Rhineura* (65°) and *Leposternon* (60°); but no particular significance can be attached to the size of the angle because it is only 45° in the small *M. capensis*.

4. The skull is shorter than in amphisbaenians which are not shovel-snouted, though not as short as in any of the three Recent shovel-snouted genera listed above.

The figures in Table 1 should not be taken as exact indicators; the parameters chosen have been selected for convenience rather than for their biological significance, and the ratios, which would doubtless vary considerably within a species (especially during ontogeny) are in each case cited for a single specimen rather than given as a mean for a series. Nevertheless they do indicate a trend. In *Listromycter* the gap between parabasisphenoid and vomer is open, *not* closed, and the orbitosphenoid is exposed in the palatal view of the skull.

Table 1 Recent and fossil amphisbaenians. A, ratios of length of facial region to maximum width of facial region. B, ratios of length of whole skull to maximum width of facial region.

Museum and number	Species	A	B
K.M.	*Amphisbaena alba*	1·18	2·79
B.M.(N.H.) R.8292	*Listromycter leakeyi*	1·48	2·40*
C.G. 3722	*Leposternon microcephalum*	1·33	2·30
C.G. 0150	*Rhineura floridana*	1·37	2·10
C.G. 3567	*Monopeltis capensis*	1·16	2·00
B.M.(N.H.) 1949.1.2.78	*Monopeltis jugularis*	1·08	1·69

* length estimated

There is another character in which *Listromycter* appears to be intermediate between 'round-headed' forms on the one hand and the 'shovel-snouted' *Monopeltis* and *Leposternon* on the other. In *M. jugularis* (the largest Recent African amphisbaenid with a spade-snout) [undescribed skull: B.M.(N.H.) Zool. Dept. no. 1949.1.2.78: Fig. 3] the posterolateral corners of the palatal exposure of the premaxilla extend back to beyond the last (4th) maxillary tooth and there contact the ectopterygoid. In *L. microcephalum* the same corners reach back only as far as the middle of the 2nd maxillary tooth and again contact the ectopterygoid. In *Listromycter* and *Rhineura* they extend back as far as the middle of the 2nd maxillary tooth but do *not* contact the ectopterygoid. In forms not shovel-snouted, the posterolateral corners of the palatal exposure of the premaxilla are not extended in this fashion; in *Blanus*, for example, they terminate at the level of the 1st maxillary tooth. We do not understand the significance of this character.

The 'shovel-snouted' *Listromycter, Rhineura, Monopeltis* and *Leposternon* show remarkably similar modifications of the skull, perhaps as adaptations to a presumably similar mode of life. (As might be expected, those adaptations are less well expressed in the Miocene form than in the three Recent genera.) However, several important differences between the four genera suggest that there is no close phylogenetic relationship uniting them all into one monophyletic group. Can we deduce anything about the more distant phylogenetic relationships that must exist between these shovel-snouted reptiles?

The most striking anatomical differences between their skulls relate to the formation of the rostral process, more specifically the arrangement of the premaxilla, maxilla, nasal, frontal and external naris. *Rhineura* is unique in that its nasals are in median contact, each of them extending from the anterodorsal border of the external naris to the midline; they are not separated from each other by the backward extension of the premaxilla, as they are in most other Recent amphisbaenians (Gans & Alexander 1962). It is important to note that all the fossil amphisbaenian skulls hitherto described (all of which date from the Lower Eocene or Middle Oligocene of the U.S.A. and have hitherto been referred to the Rhineuridae; references in Gans 1978, Estes 1983) agree with *Rhineura* in this respect. [Other alleged fossil amphisbaenians are *Crythiosaurus mongoliensis* Gilmore, 1943 from the Oligocene of Inner Mongolia and *Changlosaurus wutuensis* Young, 1961 from China. But it seems to us that the former is a primitive boid snake and that the latter is a true lizard.] In *Listromycter*, however, as in *Monopeltis* and *Leposternon*, the nasals are separated by the premaxilla, which, in all three genera, extends so far back as also to effect a partial separation of the paired frontals. In all three genera too the maxilla meets the premaxilla below the external naris. But *Leposternon* differs from *Listromycter* and *Monopeltis* in that its maxilla extends also to meet the premaxilla *above* the naris and thus excludes the nasal from the border of that aperture.

Other characters do not help very much in our present state of knowledge, seeming to be distributed in a somewhat random manner. For example, the fact that a canal enters the posterolateral corner of the nasal in all these forms except *Rhineura* might appear to have some significance, until it is observed that it is present also in *Amphisbaena alba* but absent in *Blanus cinereus*. On the other hand, the frontals are distinctly pitted in all the shovel-snouted forms except *Leposternon*, and again this character is present in *Amphisbaena alba* but absent in *Blanus*. The frontoparietal suture is straight in both *Rhineura* and *Leposternon*, almost straight in *Monopeltis capensis*, wavy in *M. jugularis*, and moderately digitate in *Listromycter*—as it is in both *A. alba* and *Blanus*. One character that is clearly of no taxonomic importance at this level is the tooth count (Vanzolini 1951*a*, *b*); in *Monopeltis capensis* there is but one premaxillary tooth and two in each maxilla (a total of five), and in *M. jugularis* there are seven premaxillary teeth and four in each maxilla (a total of fifteen). *Listromycter leakeyi* retains the maximum (and presumably primitive) tooth count of seven and five—seventeen altogether.

The phylogenetic placement of the Kenyan fossil obviously depends upon the generic arrangement of the shovel-snouted amphisbaenians, a revision of which is now under way. Meanwhile the only reasonable inference that may be drawn is that *Listromycter* is neither a rhineurid, trogonophid nor bipedid but is a member of the Amphisbaenidae; within that family it appears to be on or near the line of ancestry of *Monopeltis* (*Dalophia*) but not of *Leposternon* (*Aulura*). However, it may also be that *Listromycter* represents a separate evolutionary line; we need to examine more species of the *Monopeltis* radiation.

An interesting additional point is that one of the oldest fossil amphisbaenians known, *Jepsibaena minor* (Gilmore & Jepsen, 1945) from the Lower Eocene of Wyoming, has two anterolateral protuberances of the maxilla which are in much the same position as the maxillary bosses of *Listromycter*. In other respects, however, *Jepsibaena* appears to belong to the Rhineuridae, which suggests that the presence of similar structures in *Jepsibaena* and *Listromycter* is due to adaptive convergence.

Genus *LOPHOCRANION* nov.

NAME. Greek λόφος, the crest of a helmet; κρᾱνίον, skull. Refers to the sagittal crest on the skull roof, so well developed in the genus.

DIAGNOSIS. A medium-sized amphisbaenian with weak cranio-facial flexure; slender elongate braincase with pronounced sagittal crest widened just anterior to tip of supraoccipital; transverse crest on supraoccipital; marked lateral expansion of temporal lobe beyond braincase.

TYPE SPECIES. *Lophocranion rusingense* sp. nov.

Lophocranion rusingense sp. nov.

NAME. From Rusinga Island, the only place where the species has been found.

DIAGNOSIS. As for the genus *Lophocranion*, of which *L. rusingense* is the only known species.

MATERIAL. Two incomplete skulls in the Brit. Mus. (Nat. Hist.) Palaeont. Dept. **Holotype**, no. R.8293 (collector's field number not known). Paratype, no. R.8294 (collector's field number 33A). Figs 4–6.

OCCURRENCE. Lower Miocene of Rusinga Island, Lake Victoria, Kenya.

General

Both these fossil skulls were evidently much smaller (see Table 2 for dimensions) than that of *Listromycter*. All that remains of each is the posterior part of an amphisbaenian skull (with occiput and ear region) broken through transversely in front. Amphisbaenian skulls, of course, do not possess bony arcades; both these specimens also lack palatopterygoid flanges, quadrates and lower jaw, so that each consists of little more than a portion of the braincase itself. As far as can be determined, the two specimens are identical except in that the holotype R.8293 represents a smaller individual than the paratype R.8294 and has better delineated sutures; it is therefore likely to be ontogenetically younger. The skull of the larger individual (paratype) is broken off anteriorly not far forward of the anterior tip of the parabasisphenoid; rather more is preserved of the smaller skull (holotype), in which the transverse break runs across the top of the face, just anterior to the highly digitate fronto-parietal suture. Both specimens have been rounded off at the fractures by subsequent rolling.

Despite their incompleteness, however, sufficient of these skulls is preserved—namely, the anterior part of the braincase—to permit a comparison with the corresponding region of *Listromycter*. It is immediately evident that they are quite unlike that genus. In particular, the braincase itself is far more slender and elongate, especially the part between the hindmost processes of the frontals and the anterior tip of the supraoccipital.

The following description is based on the holotype. Any relevant differences observed on the paratype are noted (between parentheses) at the appropriate place; it may otherwise be assumed that the two fossils are alike or that the relevant part of the paratype is missing.

Skull (general description)

The cranial region of the skull, just behind the cranio-facial flexure, is transversely narrow. Enough is preserved of the apex of the face to indicate that the cranio-facial angle was approximately 20°. The lateral margins of the braincase pass backwards, at first parasagittally and almost straight and then curving outwards at an angle of about 20° to the midline. Just before they reach the back of the skull they sweep out almost laterally to the strongly projecting otic capsules. The much abraded posterior margin of the skull is very roughly convex, the otic capsules lying farther forwards than the occipital condyle. (In the paratype the posterior margin is only slightly convex, but the remaining lateral portions of the occipital condyle project posteriorly beyond this.)

Table 2 *Lophocranion rusingense*: dimensions (in mm).

	R.8293	R.8294
Length of entire specimen as preserved	11·2	9·1
Length of cranial plane	9·6	–
Transverse width at anterior end of cranial region, i.e. at fronto-parietal suture	3·0	–
Transverse width in middle of cranial region, at widest part of sagittal crest	3·6	5·5
Transverse width across otic capsules	8·4	9·2
Median height of occiput	4·4	5·5
Length of parabasisphenoid	5·3	6·5

In lateral view the skull as preserved tapers forwards. (The paratype is too short to show this.) The ventral margin is more or less straight, except for its anterior tip which inclines ventrad at some 10°. The dorsal margin slopes gradually downwards as it passes forwards in a smooth convex curve. In this aspect the posterior margin appears as a distorted L (on the right side). The vertical, shorter arm of the L is represented by a backwardly-facing surface; the near-horizontal, longer arm is represented by a surface that faces obliquely backwards and downwards. The obtuse angle of the L would have been formed by the occipital condyle, which is here broken off (but present in the paratype).

There are only two pairs of large apertures and one single one (together with some smaller foramina) in the preserved part of the skull, other than the opening of the braincase at the broken front end. Just beneath the otic capsule, on either side, lies the fenestra ovalis; the latter is closed by the stapedial footplate in these specimens, for the stapes remain in place. Farther forward and directed ventrolaterally is the large, anteroposteriorly elongate foramen for the Gasserian ganglion. The fifth, unpaired aperture is the foramen magnum (fm), in the midline of the dorsal part of the occipital surface and extending right up to its dorsal margin; as far as can be seen, this is a more or less straight-sided quadrilateral, wider above than below. (The remaining fragments of the condyles of the paratype suggest that these originally blocked the ventral third of the aperture as preserved.) On either side of the foramen magnum, at the same height as the lower margin of the aperture as preserved and lateral to the occipital condyle, is a round, much smaller canal, the jugular foramen—actually a compound foramen (see under 'Exoccipital', p. 34). Other smaller, less noticeable foramina will be described below.

The only other prominent feature of the skull is the sagittal crest. This is fairly thick from side to side in the middle part of the cranial region and becomes narrower anteriorly and posteriorly. Although pronounced, the crest is not very high. Midway along its length it bears a triradiate boss which

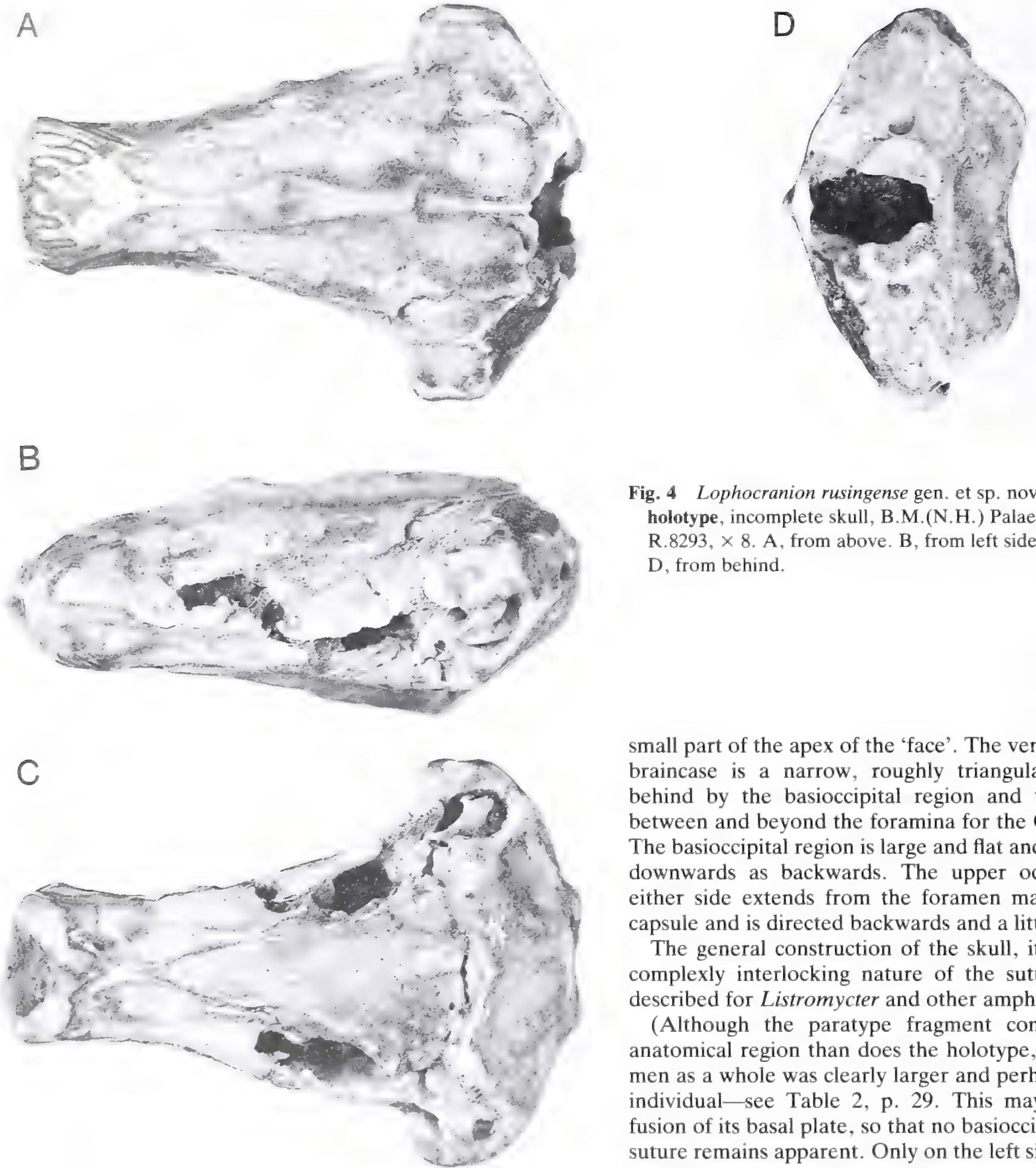


Fig. 4 *Lophocranion rusingense* gen. et sp. nov. Photographs of **holotype**, incomplete skull, B.M.(N.H.) Palaeont. Dept. no. R.8293, × 8. A, from above. B, from left side. C, from below. D, from behind.

presumably served for the usual tendinous attachments; immediately posterior to this the crest is flattened and then rises again to reach its highest point just anterior to the notch for the supraoccipital. A distinct edge at the posterior margin of the cranial roof separates it from the occiput.

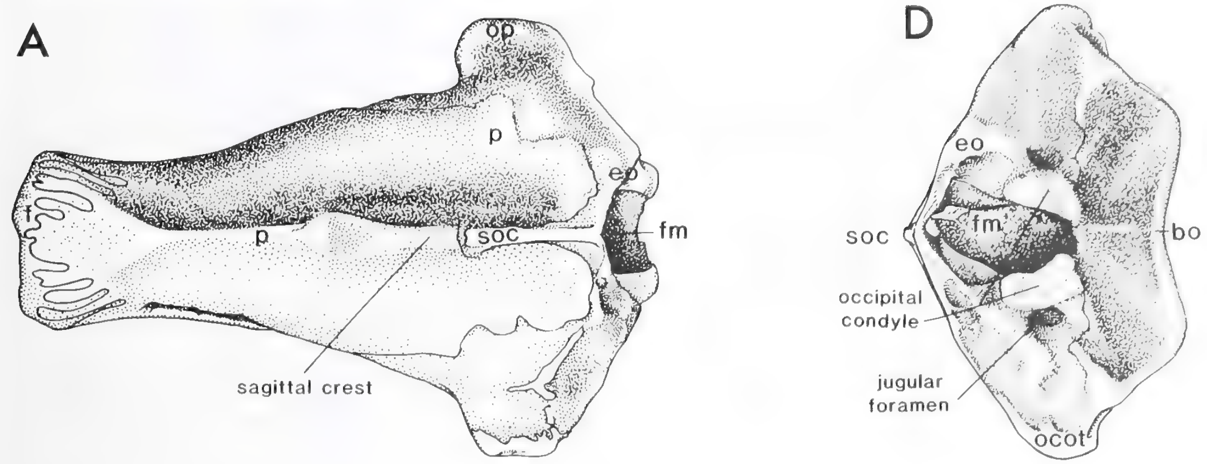
The skull as preserved has therefore seven major surfaces. On either side is the outer surface of the braincase; posteriorly these two surfaces may together be regarded as a cranial roof, extending out more or less horizontally from the sagittal crest and running onto the otic capsule. Farther forwards each descends laterally in a convex curve towards the foramen for the Gasserian ganglion (the paratype is broken here); and farther forwards still, where the braincase is very slender, it descends quite steeply towards its lower rim and might justifiably be regarded more as a lateral wall than as a roof. At the very anterior tip of the specimen as preserved is a small part of the apex of the 'face'. The ventral surface of the braincase is a narrow, roughly triangular area, bounded behind by the basioccipital region and tapering forwards between and beyond the foramina for the Gasserian ganglia. The basioccipital region is large and flat and directed as much downwards as backwards. The upper occipital region on either side extends from the foramen magnum to the otic capsule and is directed backwards and a little outwards.

The general construction of the skull, its solidity and the complexly interlocking nature of the sutures are much as described for *Listromycter* and other amphisbaenians.

(Although the paratype fragment comprises a smaller anatomical region than does the holotype, the former specimen as a whole was clearly larger and perhaps from an older individual—see Table 2, p. 29. This may account for the fusion of its basal plate, so that no basioccipital-basisphenoid suture remains apparent. Only on the left side is there a small split, the position of which suggests that it represents the remnant of a former suture between two bones.)

Parabasisphenoid (pbs) and '*element X*'

The median parabasisphenoid forms the greater part of the floor of the braincase. It consists essentially of a narrow triangle with its apex directed forwards, between and beyond the foramina for the Gasserian ganglia; the apex, which makes an angle of about 30°, is rounded off, although it may have extended farther forwards as a sharp cultriform process, the rounding off being due to postmortem rolling. The base of the triangle is the suture of the parabasisphenoid with the basioccipital; this runs more or less transversely except that on either side it makes one short, sharp zigzag halfway along its length and, in consequence, the triangle looks rather like a stylized drawing of a Christmas tree standing on a very short, wide pedestal. The external, ventral surface of the triangle is



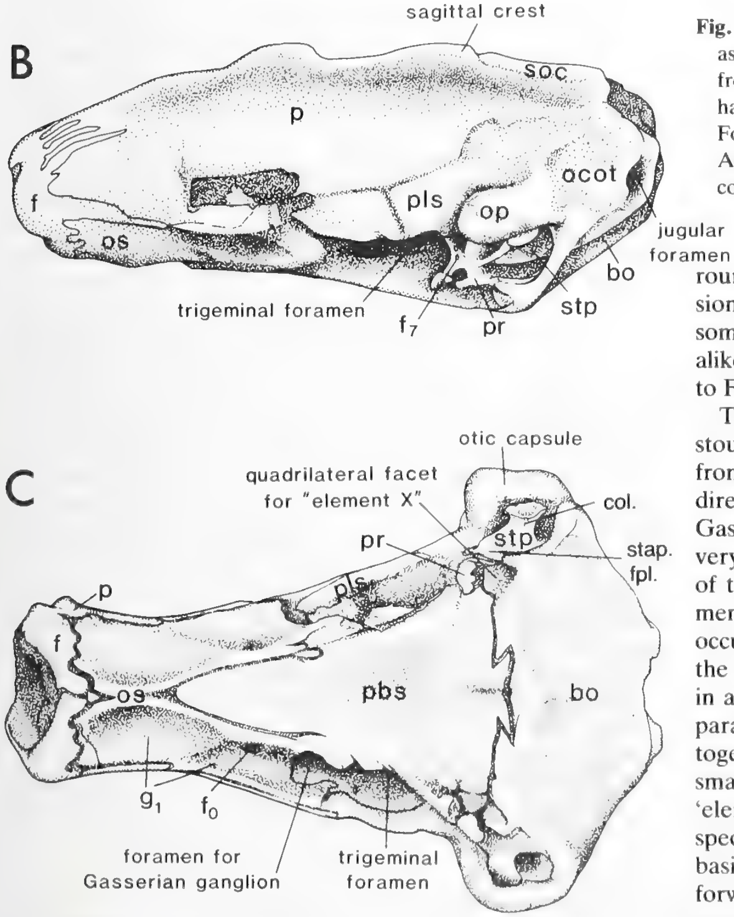
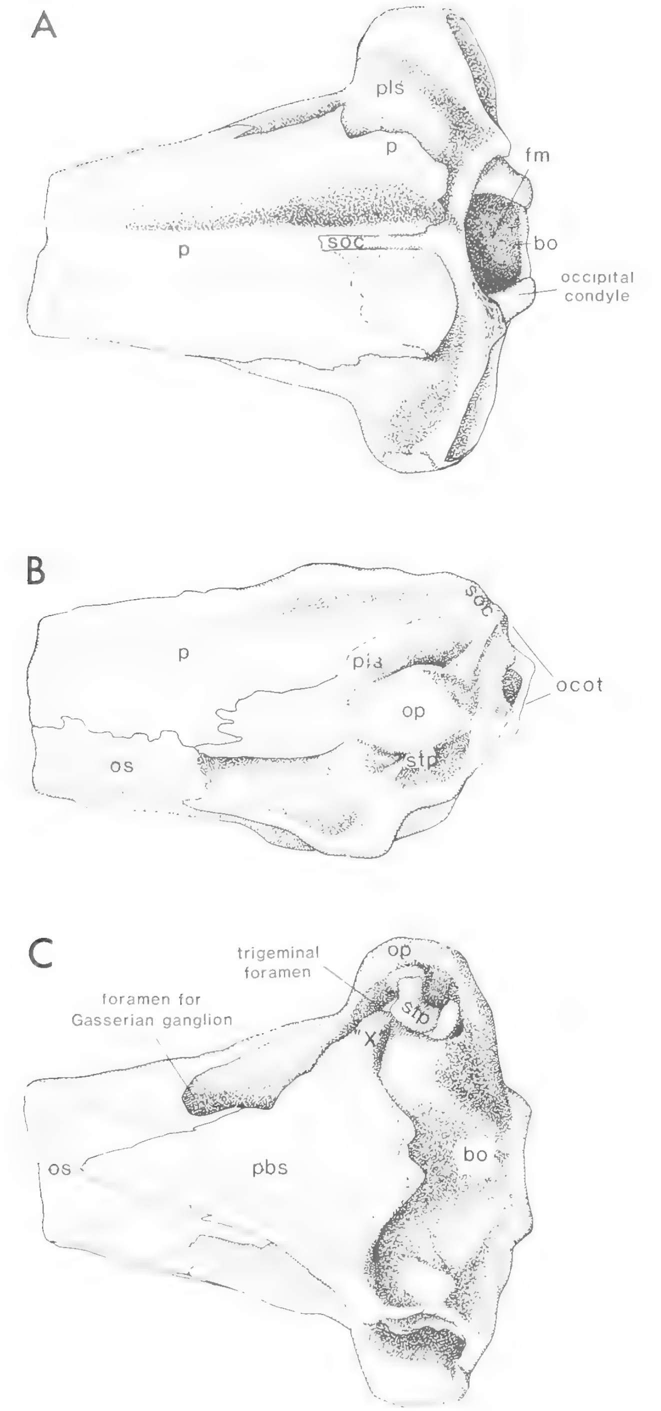


Fig. 5 *Lophocranion rusingense* gen. et sp. nov. Drawings, exactly as in Fig. 4. Many irrelevant cracks and breaks have been omitted from these drawings; further, in certain particulars, the left side has been completed from the right (and vice versa).
For key see p. 20.
Additional abbreviations on C:
col., columella; stap. fpl., stapedial footplate.

gently concave, the concavity being more transverse than anteroposterior.

The anterior third of the lateral margin of the parabasisphenoid sutures in a more or less straight line with the orbitosphenoid. At the level of the front end of the foramen for the Gasserian ganglion, however, the parabasisphenoid sends out a small lateral wing; at that point the suture between the parabasisphenoid and the orbitosphenoid becomes digitiform, terminating at the medial edge of the foramen a little way behind its anterior end. Posterior to this the parabasisphenoid forms the medial edge of the foramen; it extends dorsally and laterally on either side of the straight rounded ridge that delimits the median triangle. This extension is rather complex in form and seems to have suffered some damage, so that the two sides do not appear exactly alike; no detailed description will be attempted, and reference to Figs 5 and 6 is suggested.

The main features of the lateral extension, however, are a stout pointed process directed laterally and a little dorsally from its posterior end, and a very thin horizontal shelf directed laterally from the very edge of the foramen for the Gasserian ganglion; between the process and the shelf is a very deep channel with rounded walls. The medioventral wall of this channel is perforated by a posteriorly directed foramen which enters the cranial cavity (in the paratype the break occurs just anterior to this level). The posterolateral corner of the parabasisphenoid makes contact with the pleurosphenoid in a very complex fashion. The posteroventral corner of the parabasisphenoid and the adjacent prootic and basioccipital together bear an excavation that apparently accommodated a small bone with a more or less quadrangular base; this, the 'element X' of Zangerl (1944e, has been lost from this specimen. The articular surface for 'element X' is a deep basin-like socket, directed outwards, downwards and a little forwards; it is crossed by the relatively wide suture between parabasisphenoid and basioccipital. (It is unclear whether the element has indeed been lost from the paratype, or whether it fused to the posterior corners of the basisphenoid and abraded with these. Certainly there is no sharply defined facet and no trace of the triradial fossa.) It is also crossed by a canal, the foramen of which opens immediately anteroventral to the footplate of the stapes; the upper surface of the lost 'element X' formed the floor of the canal. (None of these canals is visible in the paratype and the entire area is solid. If the differences between the specimens are due to ontogenetic changes, one would then suspect that the absence of canals reflects either that the canals have closed, or that the fossil is broken within the 'element X' so that the canals are not exposed.)



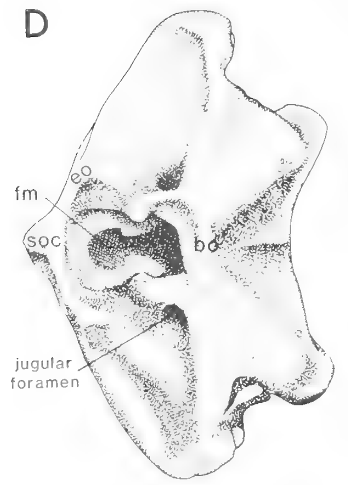


Fig. 6 *Lophocranion rusingense* gen. et sp. nov. Drawings of **paratype**, incomplete skull, B.M.(N.H.) Palaeont. Dept. no. R.8294, × 7·25. A, from above. B, from left side. C, from below. D, from behind. Many irrelevant cracks and breaks have been omitted from these drawings; further, in certain particulars, the left side has been completed from the right (and vice versa). For key see p. 20.

Orbitosphenoid (os)
The orbitosphenoid forms the ventral surface of the braincase between the region of the cranio-facial flexure and the anterior end of the foramen for the Gasserian ganglion. Its median part is underlain—and therefore covered in ventral, i.e. external view—by the parabasisphenoid triangle just described. In the midline there is a low flat-topped ridge, separating the orbitosphenoid into two halves (although there is no trace of a median suture). Anteriorly the orbitosphenoid is bounded by the frontals meeting each other in the floor of the braincase; the suture is more or less transverse but rather irregular. The lateral surface on either side is simple and externally concave; its anterior third is with a backwardly directed process of the frontal, the rest is with the parietal. Posteriorly the orbitosphenoid extends a short way along both lateral and medial edges of the foramen for the Gasserian ganglion on either side; its posterior termination on the lateral edge abuts against the anterior termination of the pleurosphenoid. Although the elongated foramen for the Gasserian ganglion ends a little anterior to this point, it continues farther forwards as a broad, shallow groove (g_1) in the ventral surface of the orbitosphenoid which curves gently outwards and tapers forwards to end near the point where frontal, parietal and orbitosphenoid meet. On the inner edge of this groove, about a quarter of the way from the foramen for the Gasserian ganglion to the frontal-orbitosphenoid suture, a small foramen (f_0)—presumably for the optic nerve—enters the bone; it is directed posteromedially.

Frontal (f)
Only the extreme posterior ends of the frontals remain; these together form a ring around the front end of the cranial region of the skull. (The frontals are missing entirely in the paratype.) They are separated from each other only by a convoluted median suture above and below the cranial cavity. Posteriorly they suture with the orbitosphenoid below, by a more or less transverse but rather irregular suture, and elsewhere with the parietal. The fronto-parietal suture is rather complex. Beginning in the dorsal midline, just below the apex of the 'face', it proceeds laterally by a series of four or five narrow interdigitations of progressively increasing length; the front ends of the interdigitations lie at about the same transverse level as the starting point, but their back ends

lie progressively more posteriorly. The first two or three are on the 'face', the last and most lateral two interdigitations are on the side of the skull. The last interdigitation of the frontal, seen in lateral view, appears to be directed backwards and upwards. From its base another process of the frontal, about as long as the last interdigitation but directed backwards and downwards, runs down between the parietal above and the lateral margin of the orbitosphenoid below. The most anterior part of the parietal, between the last interdigitation of the frontal above and this posteroventral process below, is broken off on the right side of the holotype. This break reveals that the frontal is more extensive internally and is merely overlapped by the parietal in this region; the parietal lies in a deep trough of the frontal, the bottom of which bears shallow longitudinal grooves.

Parietal (p)
The greater part of the external surface of the roof and sides of the braincase is formed by the unpaired parietal, which forms also the extreme posterior apex of the 'face'. Except in the anterior region, however, the roof and sides of the braincase are also formed in part by the fused pleurosphenoid, occipital and otic bones, henceforth to be referred to here as the occipito-otic complex (ocot). The parietal overlaps this complex posteriorly, but in the holotype described here parts of the parietal have been broken off and the resulting 'suture lines' are rather misleading; the true extent of the parietal is indicated by a depression in the occipito-otic complex which is bounded by a distinct rim. The irregular surface of the depression and the broken edges of the parietal indicate very clearly the complex interdigitating nature of the suture.

Posteriorly the parietal has a deep, very distinct median slot running forwards for about a quarter of its length; this accommodates the supraoccipital process, which thus forms the median portion of the sagittal crest in this region. The parietal-supraoccipital suture passes backwards down the side of this bar, parallel to the midline and very close to it. Just before reaching the back of the skull it curves outwards to run more or less parallel to the posterior margin of the skull roof in the region lateral to the foramen magnum. More laterally still it curves forwards again, passes medial to the otic capsule, and then continues forwards and a little downwards along the side of the braincase as the parietal-pleurosphenoid suture (in the paratype the edges are variably broken in this region); this is only very slightly irregular except in that, at its extreme anterior end, a short 'finger' of parietal points backwards and downwards towards the middle of the trigeminal foramen (the break is near the posterior third in the paratype). Forward of this point the ventral edge of the parietal reaches the lower rim of the braincase and sutures with the orbitosphenoid.

Anteriorly the parietal sutures with the frontal (missing in the paratype); this too has been described above. The sagittal crest on the parietal has already been dealt with in the general description of the skull.

Occipito-otic complex (ocot)
The posterior part of the skull is represented in this specimen by a single co-ossification, lacking apparent sutures but presumably of compound origin. Comparisons with descriptions of the skulls of lizards (Jollie 1960) and particularly of amphisbaenians (Zangerl 1944, Kritzinger 1946, Bellairs & Kamal 1980, Rieppel 1981) suggest that the complex includes the pleurosphenoid, supra- and exoccipital, pro- and opisthotic bones; except for the supraoccipital all those bones are paired. They are here described in sequence without discussion of the position of the presumed lines of suture. While we thus follow other authors, we do so with some reservations since the true nature of the complex has yet to be studied—preferably on embryological material.

Pleurosphenoid (laterosphenoid) (pls)
The pleurosphenoid region of the occipito-otic complex (cf. Rieppel 1981) seems to form a considerable part of the roof and sides of the posterior region of the braincase; but, except for the posteroventral part of the lateral wall, immediately above the trigeminal foramen, it seems likely that it was generally overlain by the parietal. In the holotype the external exposures of the pleurosphenoid-supraoccipital appear to be rather greater than this because parts of the overlying parietal—at the back end of the skull, dorsomedial to the otic capsules—seem to have been lost. (Relatively more has been lost in the paratype, where the square lateral edges of the parietal confirm that these have been broken.) The anterior termination of the pleurosphenoid (missing in the paratype) is on the lateral edge of the trigeminal foramen, a short way behind the anterior end of the latter; here it abuts against the posterior termination of the orbitosphenoid. The pleurosphenoid is delimited above by the parietal, as already described; the suture is only very slightly irregular except in that, at its extreme anterior end, a short 'finger' of parietal points backwards and downwards towards the trigeminal foramen. Ventrally the pleurosphenoid forms the more or less straight lateral edge of the trigeminal foramen and then contacts the prootic, opisthotic and supraoccipital without apparent suture.

Supraoccipital (soc)
The unpaired supraoccipital adjoins the parietal anteriorly, the pleurosphenoids anteroventrally, the opisthotics laterally and the exoccipitals below. The only suture that can be discerned, however, is the suture with the parietal, described above. The external exposure of the supraoccipital consists essentially of four regions. Most distinct is the exposure of the supraoccipital process in the skull roof, which appears as a narrow, keeled, straight-sided bar fitting into the median slot in the parietal mentioned above; its anterior end, the processus ascendens, is not tapered but ends bluntly in a straight transverse line. There is a semicircular gap around its anterior end which was presumably filled with cartilage in the living animal (as in *Dalophia* and *Monopeltis*; Kritzinger 1946, Gans personal observation) and beyond this the ridge of the sagittal crest is continued forwards by the parietal as already described. The supraoccipital itself begins to widen backwards before the parietal sutures on either side begin to diverge, i.e. the parietal overlies it laterally towards the back of the skull.

Despite the lack of sutures, it may also be presumed that the supraoccipital forms:

1. A narrow strip along the posterior edge of the skull, the roof of which is not quite covered by the parietal.
2. That part of the skull roof that is posteromedial to the otic capsule.
3. The uppermost strip of the occipital surface of the skull.

Prootic (pr)
The element that we consider to be the prootic lies behind the trigeminal foramen, of which it forms the concave posterior

border; it contacts the parabasisphenoid medially and the pleurosphenoid (without suture) laterally. Posterolaterally it contacts the otic capsule, of which it may also form a part. From this region a short, stout process descends to the socket for the articulation of the 'element X' of Zangerl (1944; see below), of which it forms the anterolateral portion (and to which it is fused in the paratype). The anteromedial portion of 'element X' is formed by the parabasisphenoid and the posterior portion by the basioccipital (all of which are fused in the paratype). The suture with the basioccipital is presumed to be represented by the canal that runs across the articulation—as described in the section on the parabasisphenoid, p. 31—although the two elements seem to be continuous at the base of the canal (fused in the paratype). Posterolaterally this element is overlain by the anterior part of the stapedial footplate. Just anterior to its contact with the stapes two small foramina, one above the other, penetrate the bone; on the left side (f_7) they are very closely adjacent, on the right they are much farther apart. (A single large oval foramen lies in an equivalent position on each side of the paratype. It is uncertain whether a second foramen is covered by the stapes, yet these do not seem to be displaced.) These, from their spatial relations to the stapes, are presumed to be the facial foramina for the VIIth nerve.

As all the elements in this region are fused together, we must give our reasons for believing this particular part to be the prootic:

1. The element forms the posterior wall of the trigeminal foramen (Romer 1956: 28).
2. It is perforated by the two small foramina that carry the VIIth nerve; these lie just anterior to the extent of the stapes.
3. It forms the anterior part of the rim of the fenestra ovalis and supports the wide anterior flange of the stapedial footplate.
4. It lies immediately anteroventral to the otic capsule.
5. It lies lateral to the lateral termination of the basisphenoid-basioccipital suture (obliterated in the paratype).

Opisthotic (op)

The opisthotic forms the greater part of the otic capsule; it is a large, solid, rounded swelling that projects laterally from the posterolateral corner of the skull roof and overlies the fenestra ovalis. No sutures are visible, either on it or around it, but it is possible that the capsule includes also a contribution from the prootic. The rounded anterior face of this process apparently formed the articular surface for the cup-shaped head of the quadrate, a bone that is missing in all these specimens. The texture of the head is rougher than that of the cranial roof; in particular, the dorsolateral half is penetrated by numerous small pits as well as by one fairly large foramen (not apparent on either side of the paratype) placed along the dorsal edge of what is here interpreted as being the articular surface.

Exoccipital (eo)

Most of the upper part of the occipital surface of the skull, facing upwards and backwards on either side of the foramen magnum, is presumably formed by the exoccipitals. As mentioned above, the uppermost strip of this surface is probably formed by the supraoccipital, but no suture can be seen. On each side a slightly irregular suture (fused in the paratype) runs from beneath the otic capsule and passes below the exoccipital to reach the bottom of the foramen magnum; beneath this is the basioccipital. The large oval occipital condyle, the back of which is strongly abraded (mostly missing in the paratype) is thus formed jointly by the basioccipital and the exoccipitals. On either side of the occipital condyle, within the exoccipital, is the jugular foramen (for the IXth, Xth, XIth and XIIth cranial nerves); while it appears as a single opening, it is actually a somewhat convoluted cup-shaped depression containing one lateral, two ventral and at least two anterior foramina penetrating deeply (these are not clear in the paratype). The exoccipital is in contact with the otic capsule, more specifically (one presumes) with the opisthotic, but again the suture is obliterated.

Basioccipital (bo)

This element forms essentially the lower part of the occipital surface (partially broken out in the paratype), a large flat area directed as much downwards as backwards. Its upper suture with the exoccipitals and its lower suture with the parabasisphenoid have already been dealt with in the respective descriptions of those bones. (All are fused in the paratype.) As also mentioned above, it contributes towards the formation of the occipital condyle. Laterally it contacts the otic capsule above and the fenestra ovalis below; indeed, it forms the posterior and ventral margins of that aperture. More ventrally still, between the fenestra ovalis and the parabasisphenoid, it contacts the prootic; together with the latter two elements it forms the socket-like articulation for the 'element X' of Zangerl (1944).

Stapes (stp)

The large fenestra ovalis is closed by the more or less oval footplate of the stapes, which seems to extend forwards beyond the margins of the fenestra. From this, directed not only outwards but also a little upwards and backwards, projects the short, laminar columella (missing on the right side of the paratype). The columella is supported by a buttress running anteroventrally.

Phylogenetic position

The phylogenetic position of *Lophocranion* is especially difficult to determine; the remains of the animal consist of little more than the braincase, which is very constant in structure throughout the Amphisbaenia. It is easier to determine what *Lophocranion* is not than what it is.

Rusinga, where the *Lophocranion* material was found, is not far outside the somewhat restricted geographical range of the Recent Trogonophidae (north-west Africa; the 'horn of Africa' and Socotra; and southern Arabia and the lands around the Persian Gulf). But the Trogonophidae may at once be excluded from consideration. *Lophocranion* has a triradiate boss on the sagittal crest which may have served for the attachment of tendons from the axial musculature; none of the trogonophids possesses that character, although it is found in several other amphisbaenians (Amphisbaenidae *sensu* Gans 1967*a*). The form of the processus ascendens of the supraoccipital is also characteristically amphisbaenid in *Lophocranion*; in the trogonophids its structure is typified by that of *Trogonophis* itself, of which Gans wrote (1960: 151) 'The processus ascendens must not be considered to be an actual process here. Because the cranial plates overlap widely rather than join by suture, the processus is actually that portion of the supraoccipital exposed between the two posterior lobes of the parietal. There is no cartilaginous plug or foramen apparent at the very tip of the processus.'

Lophocranion is therefore likely to be an amphisbaenid. But it cannot be placed among the horizontally flattened, shovel-snouted forms (a) because the anterior part of the cranial region is not shortened (it is relatively much longer even than in *Listromycter*, where the shortening is less marked than in Recent shovel-snouts), and (b) because the cranio-facial angle is only about 20°. Nor can it be placed with or near any genera with vertically compressed skulls, such as *Ancylocranium* or *Geocalamus*; in those genera the braincase is definitely oval in section, higher than wide. It is therefore probable, more specifically, that the new form is one of the more generalized, round-headed amphisbaenids.

The Recent amphisbaenids of Africa include four such genera: *Chirindia, Cynisca, Loveridgea* and *Zygaspis*. All are much smaller than *Lophocranion* (and also smaller than most of the species from South America: see Gans 1968, 1974). Indeed, none of those four African genera has a skull longer than 13 mm, whereas the total length of the skull of the *Lophocranion* holotype is estimated to have been about 17 mm (and that individual is considered to have been a juvenile, the paratype being much larger still). The braincase of *Lophocranion* appears to be altogether more slender and elongated, the distance between the fenestra ovalis and the fronto-parietal suture being greater than the distance between the fenestra ovalis and the occiput. None of the four African genera mentioned above has a processus ascendens that projects relatively as far forwards into the back of the parietal, none has a sagittal crest, and none has a braincase of the same outline (in particular, the otic capsules of *Lophocranion* seem to project more laterally, those of the Recent forms more anterolaterally). In addition, *Loveridgea* differs from *Lophocranion* in that its fronto-parietal suture is not nearly as digitiform as that of the Miocene genus, whilst that of *Chirindia* is almost straight.

On the other hand, in every one of the features mentioned above *Lophocranion* is much more like the larger South American amphisbaenids or the Cuban *Cadea*. In particular, there is little to distinguish *Lophocranion* from the South American genus *Amphisbaena*, especially from the larger species (e.g. *A. alba*) of that complex and possibly polygeneric assemblage. Resemblances lie in the pronounced sagittal crest, the widening of that crest just anterior to the supraoccipital tip, the transverse crest of the supraoccipital, and the marked lateral expansion of the temporal lobes on so slender a braincase. Indeed, we cannot yet establish any characteristics in which the preserved portions of the braincases of *Lophocranion* differ from those of *Amphisbaena*.

It must be pointed out that little is known of the variability within the genus *Amphisbaena*. Such characters as the proportions quoted above and the development of a sagittal crest may well be dependent upon absolute size or stage of ontogeny. It is also possible that the characters in question may eventually turn out to be those of large, generalized amphisbaenians, rather than autapomorphies of a derived group.

The zoogeographical importance of *Lophocranion* may not be as great as would superficially appear. It is faintly possible that we might be dealing with a 'South American' form in Africa, but much more likely that (a) the characteristics of the posterior portion of the skull are much less diagnostic at the amphisbaenian species level than are those of the anterior portion, and (b) the aspects shown here represent an earlier grade of specialization still demonstrated in the fossil and retained in South American species but lost in the present-day African forms. Similarly, some early North American rhineurids show an amphisbaenid pattern (Estes 1975). In any case, it must be remembered that the comparison is between a Miocene member of an African lineage and extant members of the South American group. In this case we had three options:

1. To leave the Rusinga form unnamed, merely describing it as 'amphisbaenid gen. et sp. indet.' This has the disadvantage of complicating citation.
2. To assign the Rusinga form to the genus *Amphisbaena*, hitherto restricted to South America. This course of action might lead to the basing of important zoogeographical conclusions upon nothing more than the posterior parts of braincases, lacking all those elements that are generally used in diagnosing amphisbaenians.
3. To give a new generic name to the Rusinga form, even though it may later prove that the species is congeneric with certain South American species of *Amphisbaena* (or with Miocene populations ancestral to them or to modern African genera).

We have chosen the third option as being the least of three evils.

On the information now at our disposal we cannot go further than this. Additional studies, and perhaps the acquisition of new material, may lead to taxonomic conclusions that are less vague; and those, in turn, may prove to have interesting zoogeographical implications.

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A revision of the English Wealden Flora, II. Equisetales

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Synopsis. The three known equisetalean species from the English Wealden are revised and type specimens selected. Their geological occurrence and stratigraphical range are discussed.

Equisetum burchardtii Dunker is known only from *in situ* rhizomes and tubers in the English Wealden, but in the German Wealden also from subterranean parts of aerial shoots. An emended diagnosis is given, a neotype chosen and a reconstruction suggested. The poorly characterized tuberous species *Equisetites yokoyamae* Seward is discussed, compared with other tuberous material and the lectotype selected. Both species were probably deciduous. *Equisetites lyellii* (Mantell) Seward, which occurs extensively *in situ* in the soil beds of the Wealden in Sussex, is known also from dispersed aerial parts in fragment partings above the soil beds. The diagnosis is emended to include cuticular and anatomical details and the lectotype is chosen. *E. lyellii* was probably winter-green. The subgeneric affinities of the fossil species are discussed in relation to comparable extant species.

Pilasporites allenii Batten, the probable spore of *E. lyellii* which is now known from dispersed sporangiophore heads, is discussed and compared to other putative equisetalean spores. Palaeoenvironments are considered and probable habitats suggested.

INTRODUCTION

Many beds in the Wealden succession of south-east England contain plant roots in positions of growth. Usually the tops of the plants have been eroded away and it is normally impossible to suggest affinities for such isolated roots, although occasionally it is reasonable to guess that they belonged to *Equisetum* or *Equisetites*. However, sometimes they are connected to excellently preserved equisetalean rhizomes, tubers and underground parts of aerial shoots, and can then be identified with confidence. Three members of the Equisetales have been described from the English Wealden: *Equisetum burchardtii* Dunker, *Equisetites yokoyamae* Seward and *Equisetites lyellii* (Mantell) Seward. From England *E. burchardtii* is known only as lengths of thin rhizomes bearing tubers, but since aerial shoots are known from the Wealden of Germany these are described and figured here. *E. yokoyamae* is very poorly characterized and may even represent only a different preservational state of *E. burchardtii*. *E. lyellii* is by far the best represented of the three species, known from an abundance of excellent material found in positions of growth and is one of the few Wealden plant species which can still reliably be found in the field. It is widely preserved *in situ* in the 'soil beds' (fossil aquatic soils of Allen, 1976) in the Wealden succession of south-east England and the bulk of this paper is devoted to the taxonomy and geological significance of this species.

The material studied belongs to several collections made by a number of people over a period of about 150 years, starting with Mantell (1833) and later Rufford (Seward 1894), but notably in this century by Allen (1941, 1947, 1976) and most recently by Batten. The collections are mainly housed in the British Museum (Natural History) (B.M.(N.H.)) with numbers prefixed V.; the Sedgwick Museum, Cambridge with numbers prefixed K.; the Museum für Naturkunde, Humboldt University, East Berlin, numbers without a prefix. The Appendix lists all the specimens figured here together with their locality, stratigraphical horizon and present location, as well as details of other interesting specimens which have not been figured.

GEOLOGICAL OCCURRENCE

Of the several Wealden formations the Wadhurst Clay, which is thought to be of Valanginian age, has yielded the most numerous *Equisetum* and *Equisetites* finds both in positions of growth and as dispersed fragments. Most of the 'soil beds' are in the Wadhurst Clay and the majority of the specimens in them are referable to *E. lyellii* without reservation. Conveniently referred to as 'soil beds' for descriptive purposes, they were undoubtedly aquatic (Allen 1976) and are discussed in more detail below. Allen (1976, Appendix I) has given a comprehensive check-list of soil horizons and their localities in the Wealden of the Weald. Details of the upper parts of the aerial shoots of the species have been obtained entirely from macroscopic stem fragments which are common in thin debris partings associated with the soil beds. Older and younger occurrences of the species are scarce, but dispersed remains of aerial stems have been found in Berriasian and Valanginian–?Hauterivian strata in the Weald. Some of the *in situ Equisetum* which has been recorded from these rocks may differ from *E. lyellii*. In particular some rhizomes are very slender; not so slender, however, as the tuber-bearing rhizomes of *E. burchardtii*. Tuberous forms of *Equisetum*, including *E. burchardtii*, are rare and, by contrast with *E. lyellii*, have not been found in the Wadhurst Clay Formation. Records so far are limited to isolated occurrences in arenaceous facies of the Ashdown Beds Formation and Weald Clay Group (Allen 1959, 1962, 1976; Kennedy & MacDougall 1969). It is clear that *E. lyellii* can have rather thin rhizomes, such as those shown in Fig. 17 from Poundsford (top Purbeck) and in Fig. 23 from the Brede Soil Bed (Wadhurst Clay). They could represent a response to less suitable environmental conditions such as an increase in salinity or more arenaceous deposition. Similar specimens from Philpots Quarry (lower Grinstead Clay) and the Hackenden Soil Bed (possibly the same horizon) are less well preserved, but can be identified with confidence as *E. lyellii* on the basis of their characteristically very short internodes. However, the possible presence of one or more completely different and as yet unrecognized species should not be ruled out because preservation is often so poor as to preclude specific identification.

Many other beds contain roots in position of growth but the plants to which they belonged are usually missing because an erosion surface supervenes. It is normally impossible therefore to suggest affinities for them, although when interbedded with deposits in which rhizomes of *Equisetum* or *Equisetites* occur, it is reasonable to guess that they too are equisetalean.

All the equisetalean material described from the Wealden of Germany by Dunker (1846) and Schenk (1871, 1876) is from localities regarded as Berriasian in age. Unfortunately all but one of their original specimens are missing.

SYSTEMATIC DESCRIPTIONS

Class **SPHENOPSIDA**
Order **EQUISETALES**
Family **EQUISETACEAE**

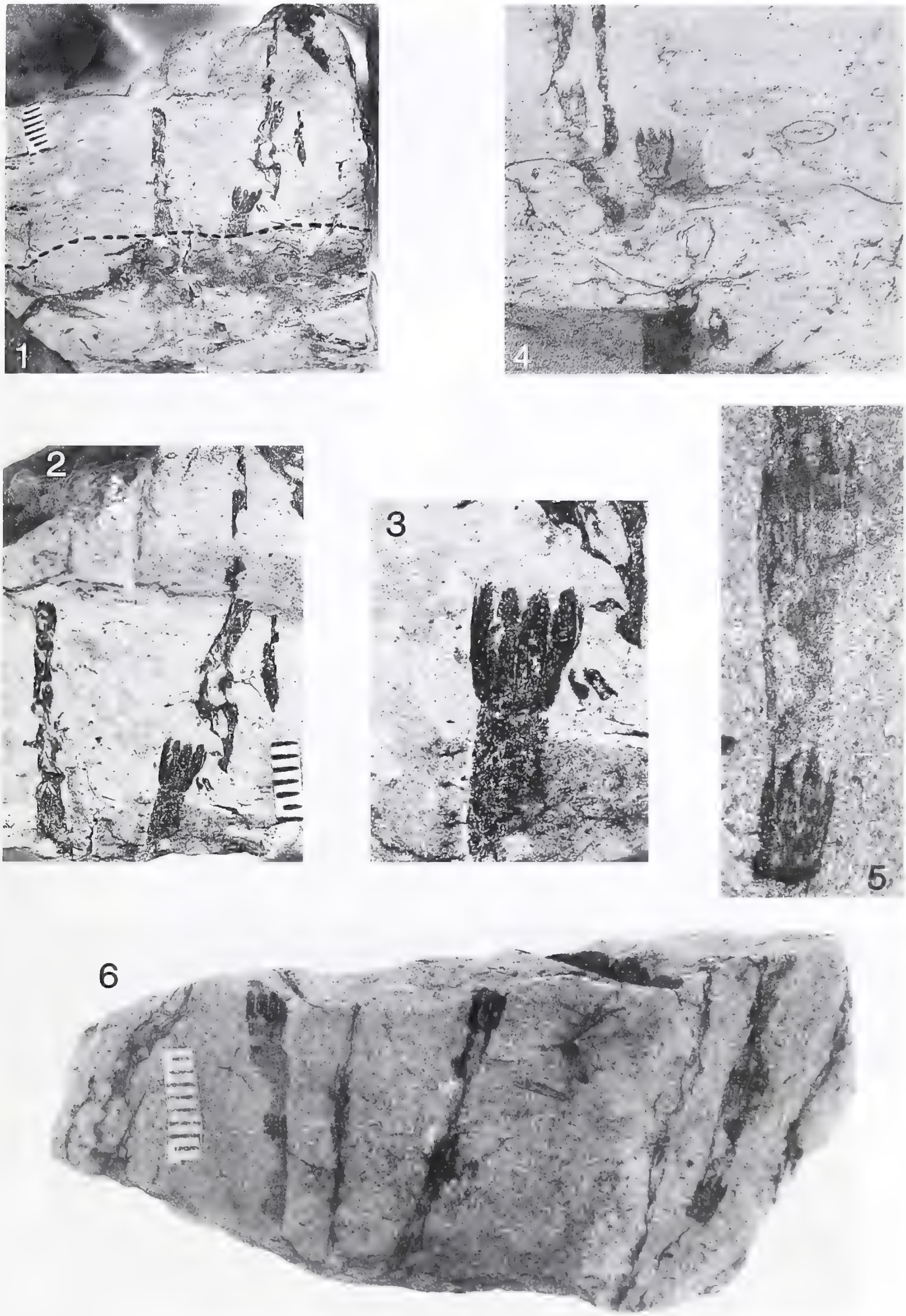
Genus ***EQUISETUM*** Linnaeus

Opinions and conventions concerning the use of the Recent genus *Equisetum* L. for fossil species have swung back and forth over the past 150 years, as the synonymies of *E. burchardtii* and *E. lyellii* show. There is a strong argument for retaining *Equisetites* Sternberg for all extinct species, however closely they resemble modern forms, and in many ways we prefer this usage. However, there has been an increasing tendency in recent years (Harris 1961, Gould 1968) to include a species, whatever its geological age, in the living genus when differences cannot be demonstrated. This is of course common practice with Tertiary plants. Although anatomical details of *Equisetum burchardtii* Dunker are not available it is so similar to living species of the genus *Equisetum* (subgenus *Equisetum*) that it is difficult to imagine that any generic differences could exist. We have therefore decided to include it in *Equisetum* L., as indeed did Dunker and Schenk.

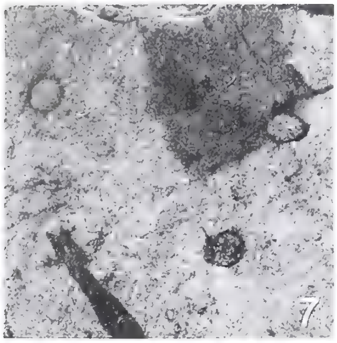
Equisetum burchardtii Dunker Figs 1–12, 14

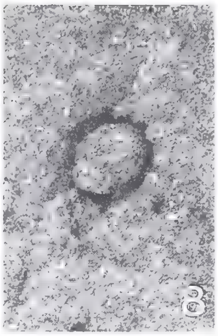
?1824 *Carpolithus Mantellii* Stokes & Webb: 425; pl. 46, figs 3, 4; pl. 47, fig. 1. (Tubers only).
?1827 *Carpolithus mantellii* Stokes & Webb; Mantell: 56; pl. 3, figs 3, 4; pl. 3*, fig. 1. (Repeat of Stokes & Webb figures).
?1833 *Carpolithus Mantelli* Stokes & Webb; Mantell: 245; text-fig. on p. 246.
1846 *Equisetites (Equisetum) Burchardti* Dunker: 2; pl. 5, fig. 7.
1846 *Carpolithus Lindleyanus* Dunker: 22; pl. 2, fig. 7 in part.
1846 *Carpolithus cordatus* Dunker: 22; pl. 2, figs 7 (in part), 10.
1846 *Carpolithus Huttoni* Dunker: 22; pl. 2, fig. 8.
1846 *Carpolithus certum* Dunker: 22; pl. 7, fig. 3.
1852 *Equisetum Burchardti* Dunker; Ettingshausen: 10; pl. 1, figs 3, 4.
1871 *Equisetum Burchardti* Dunker; Schenk: 205; pl. 22, figs 1–5; pl. 30, fig. 1 (see Fig. 10).
1876 *Equisetum Burchardti* Dunker; Schenk: 157; pl. 26, fig. 1.
1894 *Equisetites Burchardti* Dunker; Seward: 27; pl. 1, figs 5, 6.
1983 *Equisetum burchardtii* Dunker; Watson: 266; pl. 13, figs 1–3.

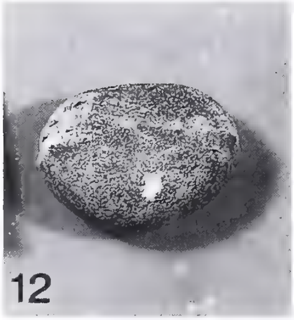
EMENDED DIAGNOSIS. Underground rhizomes 2–4 mm wide, internodes at least 3 cm long, each node bearing 2 or more ellipsoidal tubers up to 1·5 cm long. Vertical aerial shoots 2–3 mm wide arising at intervals from rhizome; internodes up to at least 3 cm long. Whorl of 8 leaves at each node on aerial

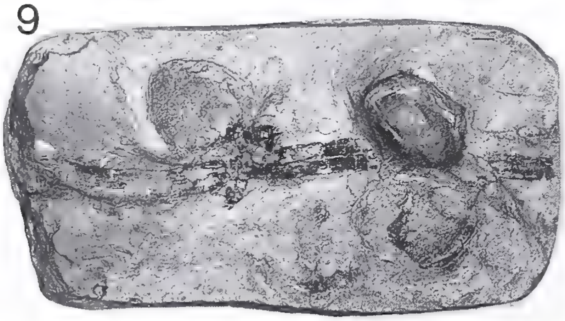


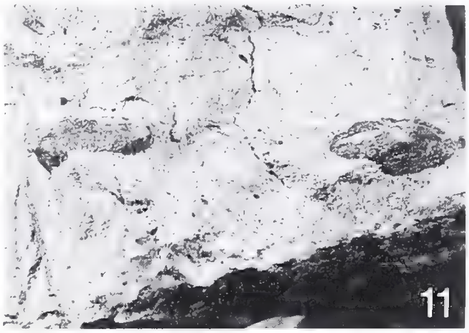
Figs 1–6 *Equisetum burchardtii* Dunker. 1, small block of sediment with plants in growth position. The dotted line marks the junction between the bedding plane (below) with rhizomes and tubers and the vertical face (above) with lower parts of aerial shoots; **neotype** (here selected). Dunker Catalogue 57, × 1. 2, vertical face of same specimen showing underground parts of aerial shoots *in situ*, × 2. 3, single shoot showing whorl of leaves with blunt tips at node; part of same specimen, × 5. 4, vertical face with various ramifying shoots, some of which may be vertically ascending rhizomes; Dunker Cat. 6, × 2. 5, aerial shoot showing sharply pointed leaves in successive whorls; Dunker Cat. 7, × 5. 6, vertical face of whole block as last, with closely spaced, well preserved underground parts of aerial shoots; see Figs 7, 8 for top surface of this block, Dunker Cat. 7, × 2.

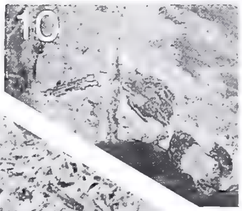


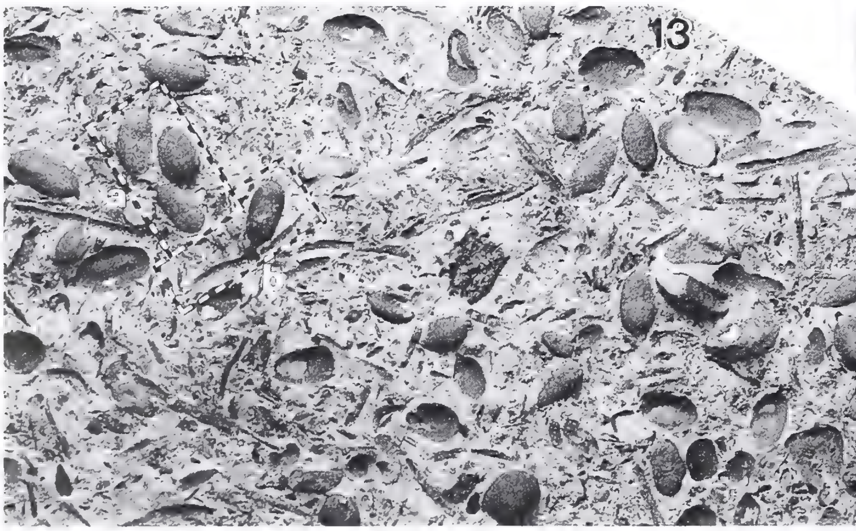












Figs 7–12 *Equisetum burchardtii* Dunker. 7, 8, top horizontal surface of block shown in Fig. 6, showing hollow stems in transverse section (compare Fig. 48, p. 52); Dunker Cat. 7; 7 × 2, 8 × 5. 9, *in situ* tubers attached to length of rhizome; V.1070, × 1. 10, Schenk's (1871: pl. 30, fig. 1) original specimen showing tubers attached to rhizome; Dunker Cat. 88, × 1. 11, *in situ* tubers from German Wealden; Dunker Cat. 87, × 2. 12, typical isolated tuber from Germany, very closely similar to numerous English specimens in B.M. (N.H.) collections; Dunker Cat. 85, × 2.

Fig. 13 *Equisetites yokoyamae* Seward. Surface of block showing portions of rhizomes and numerous tubers, may not be in growth position; see text for discussion. The dotted lines mark the areas figured by Seward (1894): a, Seward's fig. 3; b, Seward's fig. 3*. [N.B. Seward attributed the wrong specimen number to the former]. V.2335, × 1.

shoot, fused laterally to form adpressed or somewhat inflated sheath up to 5 mm long. Acutely pointed leaf tips free for more than 1 mm; well-defined commissures between leaves reaching almost to node. [Internal anatomy unknown; microscopic details unknown].

NEOTYPE. Specimen 57 in the old Dunker Catalogue, Museum für Naturkunde der Humboldt Universität, East Berlin, here selected. Figs 1–3.

TYPE LOCALITY AND HORIZON. Harrel bei Bückeburg, northwest Germany. Berriasian.

ENGLISH MATERIAL. The only English specimens so far reliably identified as *E. burchardtii* are those in the B.M.(N.H.)

collected by Rufford. They are merely recorded as being from Ecclesbourne, near Hastings, and therefore their exact horizon is in doubt. They could have come from either the Ashdown Beds Formation or the Wadhurst Clay Formation and thus may be either Berriasian or Valanginian in age. It seems most likely that they are from the Ashdown Beds as there are no other records of tuberous rhizomes from the Wadhurst Clay (Allen 1976: 428).

DESCRIPTION. The true identity of the specimens described as fruits by Stokes & Webb (1824) and likened to palm kernels by Mantell (1827, 1833) is not known, but they were almost certainly isolated *Equisetum* tubers of which there are many in the B.M.(N.H.) collections (Fig. 12). Such tubers attached to *Equisetum* rhizomes (Fig. 9) were not described from the English Wealden until much later (Seward 1894), when they were identified with *Equisetum burchardtii* Dunker (1846) from the Wealden of Germany, where they are known also from aerial shoots. There is no doubt about the specific identity of the material described by Seward (1894), but in the absence of the Stokes & Webb specimens we retain Dunker's specific epithet. Dunker (1846) at the same time erected a number of *Carpolithus* species, also probably isolated *Equisetum* tubers. Unfortunately none of Dunker's figured specimens have been recognized in any of the German collections, but the old Dunker collection in the Museum für Naturkunde, East Berlin, still has several excellent small blocks showing *in situ* rhizomes, tubers and aerial shoots. One of these (Figs 1–3) is here selected as the neotype for *Equisetum burchardtii*. This block has rhizomes, fine roots and tubers on the bottom horizontal face (Fig. 1, below the dotted line) and portions of aerial shoot on one of the vertical faces (above the dotted line). One of the aerial shoots (Figs 2, 3) clearly shows the details of a leaf sheath, with a whorl of probably eight leaves. This particular specimen has eroded leaf tips but other specimens (Figs 4–6) show acute, sharply pointed, intact tips. The shoots shown in Figs 5 and 6 have several successive nodes intact and therefore the internodal length has been taken from here, though of course these specimens must represent only the extreme basal portions of aerial shoots.

No microscopic details of *E. burchardtii* have been obtained. All attempts at making cuticle preparations were unsuccessful. As with *E. lyellii* the cuticle is rendered featureless by oxidative maceration. Our best hope is to obtain newly collected, naturally oxidized fragments now that several of the old German Wealden localities have been reopened (Riegel *et al*. 1986).

DISCUSSION. The specimen of *E. burchardtii* in Fig. 9 with thin rhizomes, long internodes and bearing tubers at the nodes is strikingly like the living species *Equisetum palustre*. The known parts of the aerial shoots may also be compared to such a species with few facets (leaves); typically five in *E. palustre* (Hyde *et al*. 1969: fig. 26) and eight in *E. burchardtii*. All the known features of *E. burchardtii* point very strongly to it being a typical species of the genus *Equisetum* subgenus *Equisetum*. All extant members of this subgenus are deciduous, with soft, easily broken aerial shoots which decay at the end of each growing season, whilst bearing food storage tubers on the rhizomes which, in all but one species, lack a central canal. The presence of tubers therefore indicates that the fossilization process began during the winter after the deciduous aerial stems had died down. Thus it is clear that the *in situ* shoots attached to tuberous rhizomes were the underground parts and of course a seasonal climate is strongly indicated, supporting the conclusions of Batten (1975) and Harris (1981) from other palaeobotanical evidence, and Allen (1976) on sedimentological grounds. It seems probable that *E. burchardtii* displayed other features typical of its subgenus. In the suggested reconstruction in Fig. 14 we have incorporated some of these likely features, such as solid, strongly angular branches distinct from the main axis and cones with rounded tops. The choice of monomorphic habit with cones borne at the apices of the green shoots is purely arbitrary.

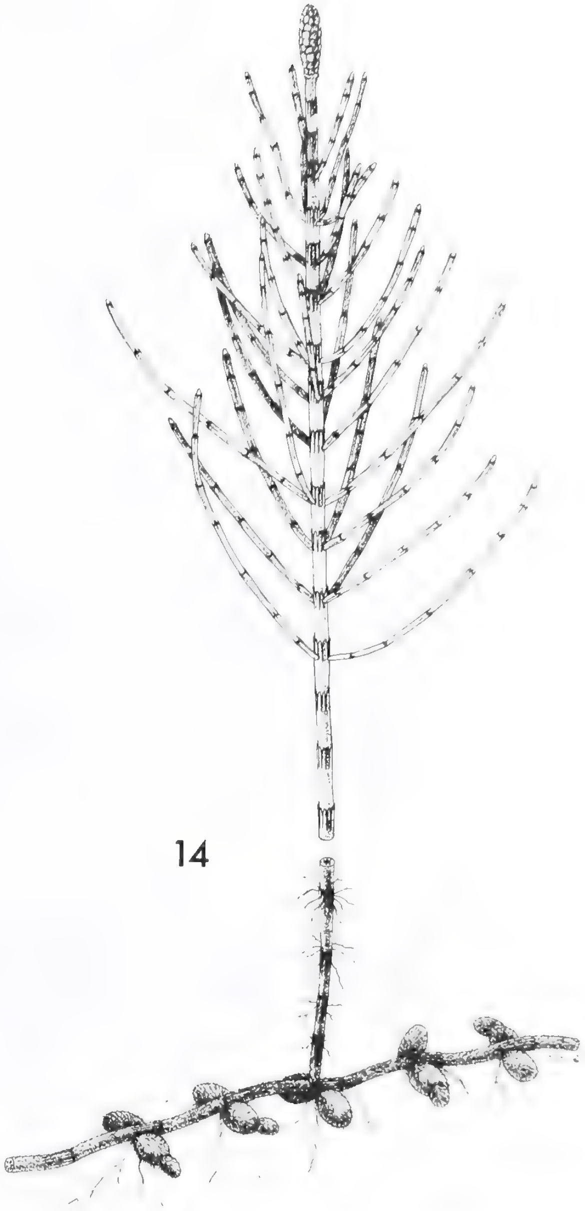

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Fig. 14 Suggested reconstruction of *Equisetum burchardtii* Dunker. Approximately × ½. © Joan Watson, 1990.

COMPARISON. For comparison with other tuberous rhizomes from the English Wealden see below under *Equisetites yokoyamae*, p. 42.

Equisetum burchardtii has been listed in several floras from different parts of the world but it is impossible to assess the reliability of the identifications. Most similar are some of the specimens, including tuberous rhizomes, which Fontaine (1889, 1905) described from the Lower Cretaceous Potomac Group of the U.S.A., ascribing them to various species. Berry (1911) redescribed this material and transferred some of it to *E. burchardtii*, but unfortunately the whereabouts of the specimens is now unknown.

E. burchardtii is distinct at the subgeneric level from the Wealden species *Equisetites lyellii*, which shows significant differences from all the living species and is discussed in detail below. From what we know about *E. burchardtii* it is more similar to living members of the group than to any of the other Mesozoic species which are known in comparable detail.

Genus *EQUISETITES* Sternberg

1833	*Equisetites* Sternberg: 43.
1894	*Equisetites* Sternberg; Seward: 23.
1961	*Equisetum* Linnaeus; Harris: 14.
1968	*Equisetum* Linnaeus; Gould: 155.

The genus *Equisetites* Sternberg was put into synonymy with *Equisetum* Linnaeus by Harris (1961), who considered that morphologically none of the fossil forms assigned to *Equisetites* could be separated at the generic level from extant *Equisetum*. This is probably true for most of the species hitherto described, but that is not to say that *Equisetites* should not be retained for use as it was originally intended, that is for plants which cannot positively be assigned to the living genus. We therefore propose its reinstatement and are retaining within it two of the Wealden species.

Equisetites yokoyamae Seward is so poorly characterized that it really does not warrant a name change on the basis of the information available, and *Equisetites* seems a perfect repository for it. *Equisetites lyellii* (Mantell), on the other hand, is now known in considerable detail including its anatomy. The evidence shows that the anatomical features of *E. lyellii* are rather further removed from modern *Equisetum* than the external morphology suggests, and in the light of this we prefer to retain it within *Equisetites* Sternberg.

Equisetites yokoyamae Seward Fig. 13

1894 *Equisetites Yokoyamae* Seward: 33, text-figs 2, 3.

HOLOTYPE. V.2335, B.M.(N.H.)

TYPE LOCALITY AND HORIZON. Ecclesbourne near Hastings. Berriasian or early Valanginian; see comments above about the age of *E. burchardtii* and the Ecclesbourne locality.

DESCRIPTION AND DISCUSSION. Fig. 13 shows part of the block of red-stained fine white sandstone covered with tubers and lengths of very thin rhizome, on the basis of which Seward (1894) erected the species *Equisetites yokoyamae*. The dotted lines on Fig. 13 indicate the areas figured by Seward (1894: figs 3, 3*). Almost all the material attributed to *E. yokoyamae* by Seward is in this same matrix and could represent a single occurrence found by P. Rufford and subsequently distributed to various museums. The tubers are much smaller and narrower than most of those of *E. burchardtii* (Fig. 9) from the English Wealden but the German material (Figs 10–12) shows a wide range in variation of tuber size. Fig. 10 illustrates the sole remaining German figured specimen (Schenk 1871: pl. 30, fig. 1), which is very close in shape and size to *E. yokoyamae* and could represent the same species in a different preservational state. However there are a few other specimens in the B.M.(N.H.), tentatively attributed by Seward to *E. yokoyamae*, which have extremely small tubers and thin rhizomes (see Appendix). The extreme difference in size between these and the largest *E. burchardtii* tubers must indicate the presence of more than one species. But, in the absence of cellular detail and without information from aerial parts, the exact nature of *E. yokoyamae* remains uncertain.

Other tuberous rhizomes recorded by Allen (1976: 427) from the Weald Clay are unlikely to be either *E. burchardtii* or *E. yokoyamae*. Those from the Slinfold Soil Bed have rhizomes about 1 cm in diameter, whereas the fattest rhizomes of *E. burchardtii* barely reach 4 mm. Specimens from the Vann Lane Sand have rhizomes 1·5 cm across and the tubers are rounded rather than elongate (Allen, personal communication). It seems likely that several herbaceous, tuberous species of *Equisetum* were present in the Wealden flora.

Equisetites lyellii (Mantell) Seward Figs 15–42, 45–51, 53–55, 57–63, 67

1833	*Equisetum Lyellii* Mantell: 245, figs 1–3. (Rhizomes figured as aerial shoots).
1846	*Equisetites Phillipsii* Dunker: 2; pl. 1, fig. 2. (Poor figure of fat rhizome).
1871	*Equisetum Phillipsii* Dunker: Schenk (*pro parte*): 206; pl. 22, figs 6–8; *non* pl. 22, fig. 9. (Rhizomes in their fattest form).
1871	*Equisetum Lyelli* Mantell; Schenk: 207; pl. 22, figs 10–12. (Rhizomes of medium size).
1894	*Equisetites Lyelli* (Mantell) Seward: 24; pl. 1, fig. 4. (Mainly list of material in B.M.(N.H.) collections).
1913	*Equisetites lyelli* (Mantell); Seward: 85; pl. 11, figs 1a, 1b.
1941	*Equisetites lyelli* (Mantell); Allen: 362, text-figs 54–56; pl. 24. (*In situ* material with new diagnosis and full synonymy including doubtful identifications).
1947	*Equisetites lyelli* (Mantell); Allen: 303, text-fig. 57. (Soil beds and rhizomes showing vascular strands).
1983	*Equisetum lyellii* Mantell; Watson: 265; pl. 13, figs 5–8; pl. 14, figs 1–7, 9–12. (Including preliminary description of stomata and sporangiophore).

DIAGNOSIS (emended after Allen, 1941). Underground rhizomes horizontal, thick, usually unbranched, with large central canal, having internodes of variable length and width, internode length 5 mm to 3 cm or more, width less than 1 cm to over 2 cm. Hollow erect stems arising singly or in pairs with internodes typically 7 mm long and 7 mm wide in the lower subterranean part, tapering to 3 mm long and 2·5 mm wide in the upper aerial part; some nodes of aerial shoots bearing whorls of narrow branches. Central canal of aerial shoot large, surrounded by a ring of vascular bundles with crescent-shaped metaxylem, tracheid thickenings probably annular. Cortex with ring of vallecular canals, oval in section [vascular bundles and vallecular canals presumed to equal leaves in number]. Leaf sheath varying from half as long to nearly as long as internode, composed of slender tapering leaves united to near their toothed apices by commissures with strongly sculptured surface; commissures extending backwards from node. Whorls of up to 46 leaves on rhizome, 26 on the lower

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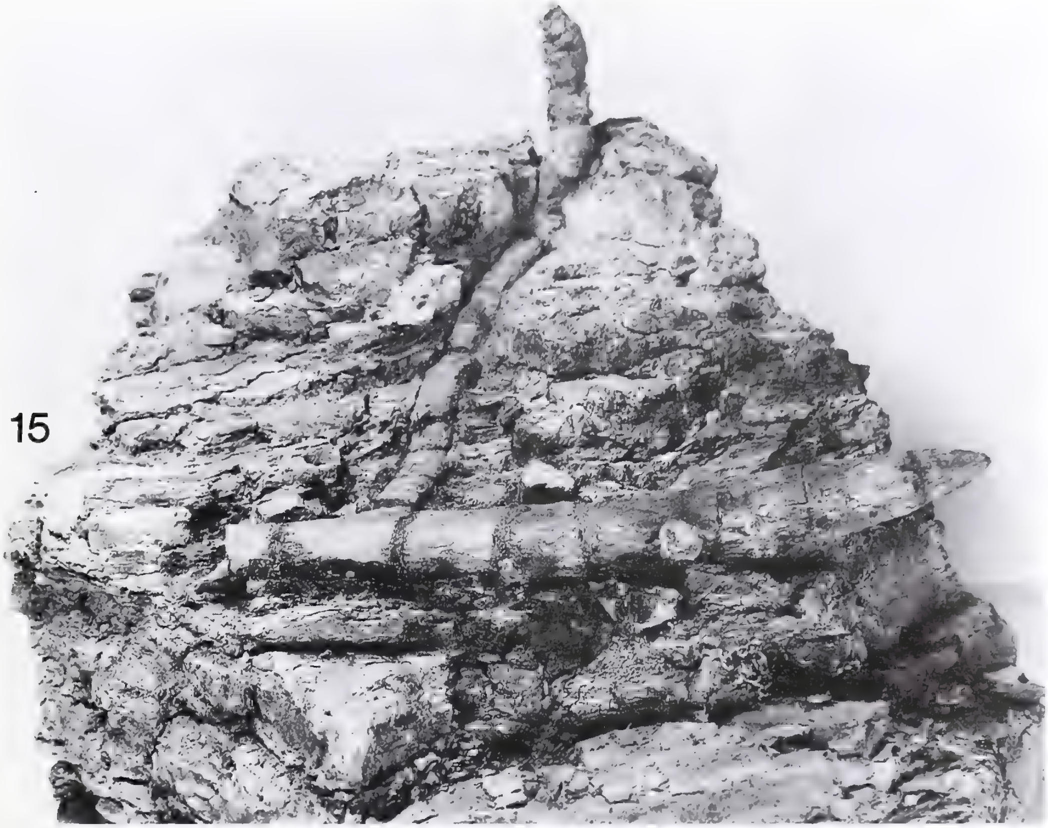

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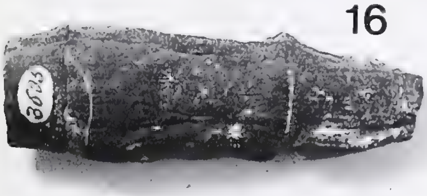

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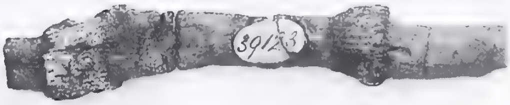


Figs 15–17 *Equisetites lyellii* (Mantell). 15, Allen's (1941) specimen of a rhizome with growing tip and aerial shoot preserved in growth position; specimen now broken, printed from original negative; K.2221, × 1. 16, 17, the two remaining original specimens figured by Mantell (1833). 16, **lectotype** (here selected), 3605, × 1. 17, 39123, × 1.

and 18 on the upper parts of the erect stems. Tubers not formed.

Ordinary epidermal cells of internode in longitudinal files, rectangular with sinuous walls marked with tranverse ridges; features less apparent in longer, narrower cells of leaf sheath. Broad longitudinal band of scattered stomata in lower part of each segment of leaf sheath on aerial shoot; stoma oval, typically 40 μm long and 20 μm wide; outer stomatal cells level with surrounding surface, ornamented with beaded sculpture along slit-like aperture and around distal margin.

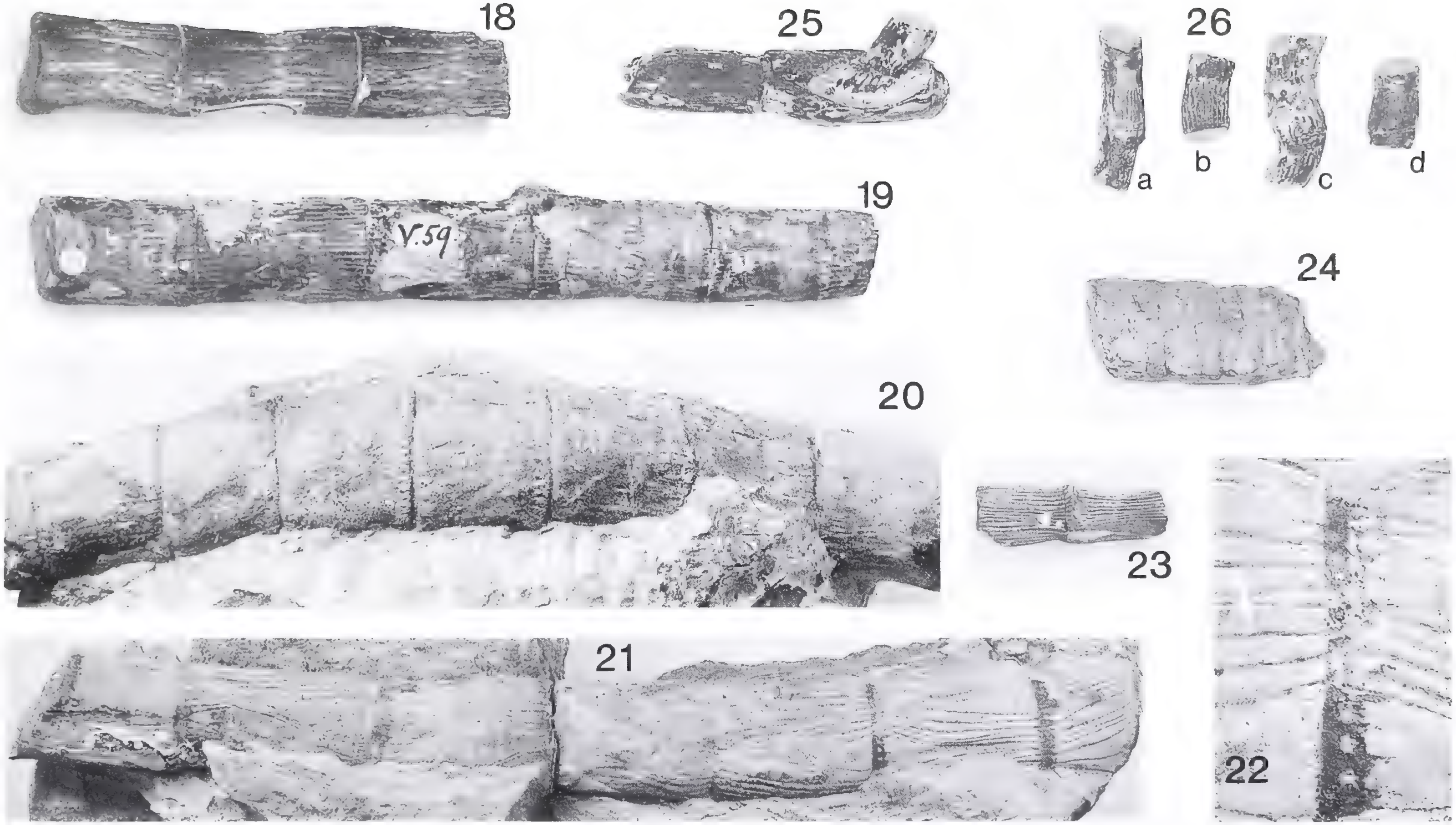
Sporangiophore peltate, head circular with about 24 surface ribs radiating from centre; epidermal cells rectangular with sinuous walls parallel to ribs. Sporangia rounded [number unknown], containing spores of *Pilasporites allenii* Batten.

LECTOTYPE. Specimen 3605 in the B.M. (N.H.), here selected. Figured by Mantell (1833: 245, fig. 3). Fig. 16.

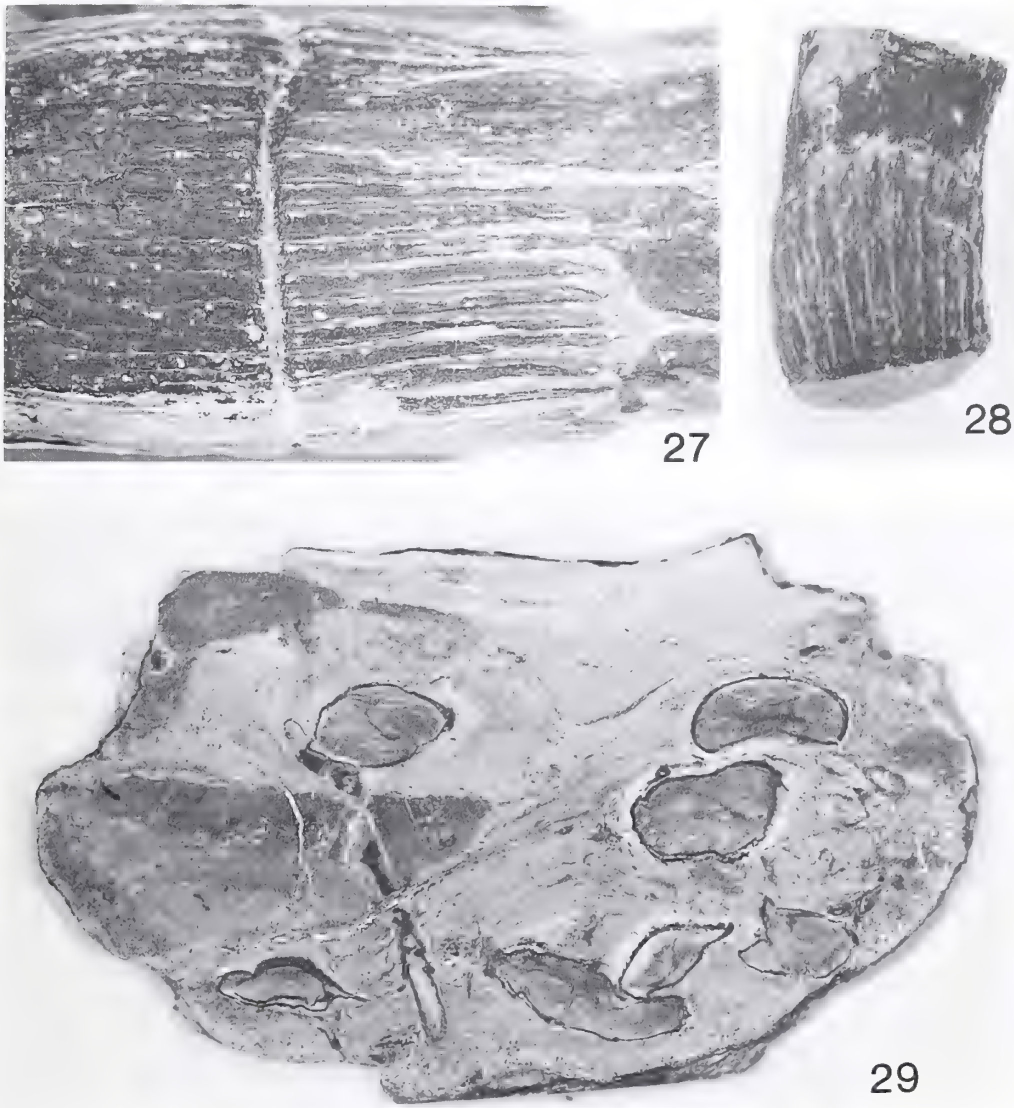
TYPE LOCALITY AND HORIZON. The locality given by Mantell (1833) as Pounceford was later confirmed by Hunter (1835) and Topley (1875: 498) as being Poundsford, south of Burwash Common, E. Sussex (TQ 637225). Poundsford lies athwart the Purbeck–Ashdown boundary and the quarries from which the specimens apparently came were in the top Purbeck (Topley 1875: 37–41, 408), of presumed Berriasian age.

STRATIGRAPHICAL RANGE. The material from the type locality is the oldest recorded occurrence of *E. lyellii*. The youngest stratigraphically are specimens from the Hackenden Soil Bed within the Grinstead Clay Member of the Tunbridge Wells Sandstone Formation, in the upper part of the Hastings Bed Group.

MATERIAL. The material studied comes from numerous localities (see Appendix) and horizons and consists of the following parts of the plant: a large number of lengths of underground rhizome found *in situ* in various states of compression or as internal moulds; short lengths of underground parts of aerial shoots, also *in situ* and often attached to the rhizome; two separate but related finds of petrified underground parts in a carbonate matrix; presumed erect axes from above ground



Figs 18–26 *Equisetites lyellii* (Mantell). All except Fig. 22 × 1. 18–25, rhizomes showing different preservation states and typical variation in width and internode length. 18, 19, rhizomes with well preserved leaf-sheaths and the longest internodes; 18, V.710; 19, V.59. 20, the fattest rhizome known, V.45457. 21, internal mould of hollow rhizome showing impressions of vascular strands along internodes, V.51137. 22, single node of same specimen showing apparent leaf-gaps, × 4. 23, narrow rhizome of similar preservation showing vascular bundles as ferruginous grooves (see Allen 1947: fig. 57A), K.2139. 24, shortest internodes known, probably close behind growing tip missing from right, V.63058. 25, rhizome with aerial shoot apparently emerging below node, V.28642. 26, portions of aerial shoots with well preserved leaf-sheaths and typically retaining circular section; a, V.63070; b, V.28643; c, V.63071; d, V.63072.



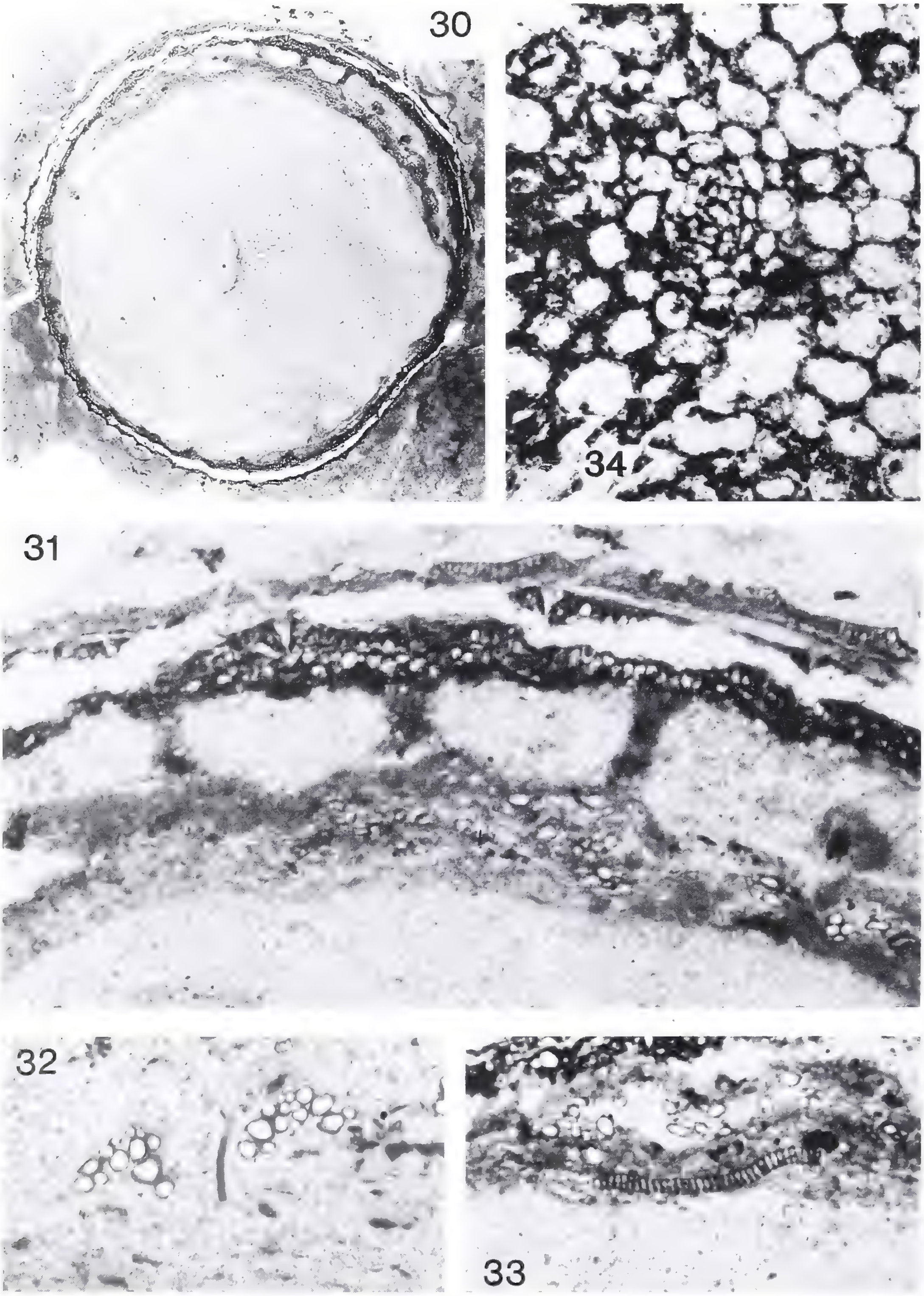
Figs 27–29 *Equisetites lyellii* (Mantell). 27, portion of rhizome showing large number of leaves in whorl with pointed tips intact; V.710, × 4. 28, portion of aerial shoot with eroded tips of leaves; V.28643, × 4. 29, vertical cut face of carbonate nodule containing rhizomes with well preserved cellular structure; V.63059, × 1

level which are known only from fragment partings in compression form; the probable spores both dispersed and from sporangiophores. Unfortunately the aerial parts are those about which we know least and organic connection has not strictly been proved. The dispersed spores are also identified only on evidence of abundant association.

All the material is from the English Wealden. *E. lyellii* is present but uncommon in the German flora.

DESCRIPTION. Figures 15–28 illustrate the easily recognizable and most characteristic features of *E. lyellii*: the thick horizontal rhizomes with a large central canal and a large number of leaves, up to 46 per node; the narrower upright stems also with a large number of leaves; the very short internode length of both rhizome and aerial shoot. The absence of tubers must also be regarded as diagnostic.

When Mantell (1833) first described *Equisetites lyellii* he failed to distinguish between rhizomes and aerial parts and did not recognize that the specimens were in growth position. This was first recognized by Allen (1941). Two of Mantell's original specimens are shown in Figs 16 and 17. The former, which has been selected as the lectotype, is a clearly recognizable portion of rhizome with one whole and two half internodes, elliptical in cross section. The tip of the specimen (Fig. 16, right side) which Mantell (1833: fig. 2) figured vertically as the 'cryptogamous head' is a broken, squashed, hollow internode. Specimen 39123 (Fig. 17) is more problematical, being very poorly preserved with incrustations of heavy mineralization. On the basis of the internode length we are inclined to think that this is also a piece of rhizome, although it is at the lower limit of recorded rhizome width. However, the specimen in Fig. 23 (collected and figured by Allen, 1947: fig. 57), which is very little wider, is without doubt a portion of rhizome, though with much shorter internodes. A third specimen (3579) in the B.M.(N.H.), which has the same poor preservation, is possibly the original of Mantell's figure 1



Figs 30–34 *Equisetites lyellii* (Mantell). All sections prepared from carbonate nodules. 30, transverse section of aerial shoot indicating large central canal and vallecular canals; V.44953, × 10. 31, portion of same section showing ridged stem surface, cells of cortex, vallecular canals and vascular bundles out of place; × 50. 32, t.s., vascular bundles showing more extensive xylem than in living species; phloem was probably present between the arms of the V-shaped xylem; V.44951, × 50. 33, displaced tracheid seen longitudinally, showing thickenings; V.44953, × 50. 34, part of cortex shown in Fig. 35, with small subsidiary trace of uncertain nature, discussed on p. 49; V.44949, × 400.

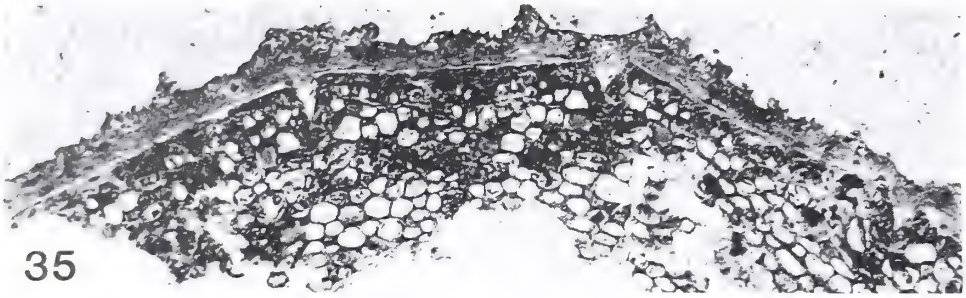
(1833), but is less easily recognizable than the other two. About a dozen other rhizomes with this same preservation survive; probably all were collected by Mantell at Poundsford. Four of them (see Appendix for details) are of particular interest in that they retain their original circular cross section. The hard, blue-grey calcareous matrix with a metallic ring which fills the rhizomes is probably one of the 'Blue limestones' of Topley (1875: 37). It seems likely that early lithification by calcium carbonate forming locally in the mud before compression produced incompressible patches. One of the four rhizomes is circular for half its length but shows considerable compression in the other half without lateral spreading (see Allen, 1947). Allen (personal communication) has observed similar partially uncompressed rhizomes in the field, associated with various lateral changes of lithology.

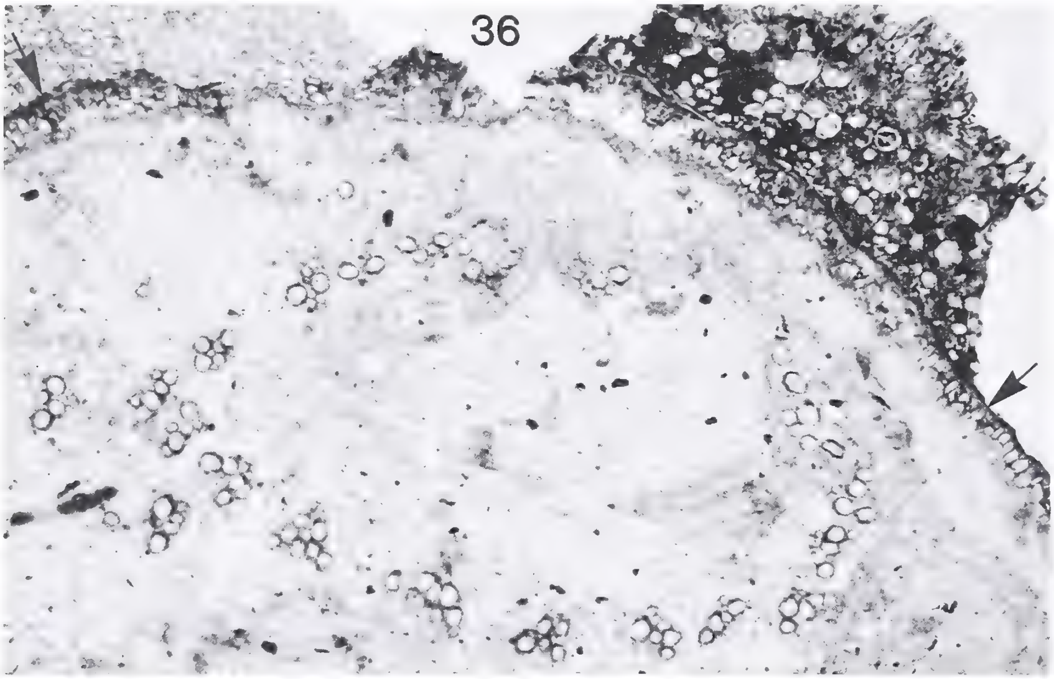
Since Mantell's time *E. lyellii* in growth position has been collected extensively by Allen, Batten and others in the numerous soil beds in the Wealden of Sussex. Material collected and studied by Allen (1941, 1947) included the splendid specimen from the Brede Soil Bed (Wadhurst Clay) illustrated in Fig. 15, which shows the rhizome complete with growing tip and an extensive length of the subterranean part of an upright stem. Unfortunately the growing tip and most of the aerial shoot are now missing from this specimen (Sedgwick Museum, K2221) and Fig. 15 has been printed from one of Allen's original glass plate negatives. Allen's description of *E. lyellii* (1941) based on the *in situ* soil bed material is very comprehensive, and apart from SEM studies of the cuticle can be little improved upon. The new information presented here comes largely from two other sources; compressions of aerial parts dispersed in the fragment beds and anatomically preserved material in carbonate nodules (Fig. 29) found by P. J. Whybrow and C. H. Shute of the B.M.(N.H.) in the Balcombe (= High Brooms) Soil Bed in the upper Wadhurst Clay near East Grinstead.

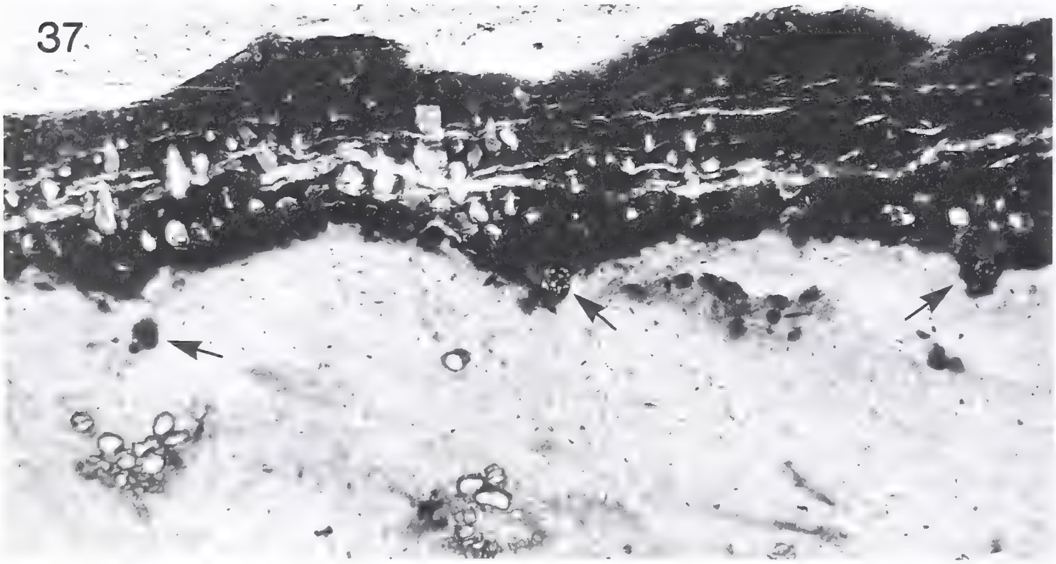
The epidermal details of the subterranean parts, which of course lack stomata, were figured by Allen (1941). Indeed cuticle preparations are easy to obtain, although they very rapidly deteriorate in acid, becoming so featureless that no cell outlines can be seen. The cells and their bars of thickening (Figs 45–49) are best seen in naturally oxidized fragments. Some of the best dispersed fragments, from the Cuckfield No. 1 borehole (Lake & Thurrell 1974), have yielded details of the stomata which were hitherto unknown. The stomata are scattered in a wide band (Fig. 40) in the flat areas of the leaf sheath between the commissures (Fig. 39). Fig. 39 shows part of a well-preserved leaf sheath from the borehole. This specimen has well-preserved stomata, two of which are shown in Figs 41 and 42. The outer stomatal cells are seen to be level with the surface and have beaded ornamentation around the perimeter and along the stomatal slit. Amongst living species we found strikingly similar stomata (Figs 43, 44) in *Equisetum sylvaticum*. It seems reasonable to suppose, therefore, that the stomata of *E. lyellii* have the same unusual construction as in living *Equisetum* (Hauke 1957, Chatterjee 1964, Page 1972*a*), the guard cells being completely covered and hidden by the two subsidiary cells which are seen at the surface. These are usually referred to as the 'stomatal cells'. Both the distribution and form of the stomata are features of taxonomic significance which will be further discussed below.

Figure 53 shows the freshly split surface of a block of fragment bed photographed under paraffin. Surfaces such as this have provided valuable new information about the subaerial parts of *E. lyellii* but have also posed problems to which we have as yet no answers. Most prominent amongst the various dispersed remains on these blocks are the so-called nodal diaphragms (Figs 53, 55). These wheel-like bodies are familiar from almost all fossil equisetalean species (Harris 1961, Gould 1968) although no such structure is known in living species. Watson (1983) has already indicated that we have reason to call into doubt their real nature, and to suggest that they may often, if not always, be a preservational effect. During the course of this study several specimens of *Equisetum telmateia* obtained for epidermal preparations were kept in a polythene bag in a dry, centrally heated room for several months. Apart from obvious changes in colour and dryness the plants remained ostensibly intact. However, upon removal from the bag and subsequent handling, they all fell apart into single internodes with a leaf sheath at the top node and a 'nodal diaphragm' at the bottom node as shown in Fig. 56. Clearly the drying and shrinking of the hollow stem had caused it to shrivel inwards a few mm above the node whilst the node itself remained as a firm ring. This has had the effect of making the vascular bundles between the vallecular canals appear as spokes radiating from the centre, presenting an unmistakable similarity to the nodal diaphragms so well known in fossil *Equisetum*. It is easy to see that during preservational degradation this resistant structure could readily become detached and rotate through 90°, the position in which the diaphragms are commonly preserved (Harris 1961: figs 4D, 5C). The nodal diaphragms found associated with *E. lyellii* are all 2 mm or less in diameter, and are almost certainly from slender branches which are one of the least known features of this plant. Allen (1941) reported seeing only one branch, about 2 mm across, but further evidence of extensive branching in some shoots comes from the specimen shown in Fig. 50 and from a number of specimens such as that in Fig. 48. The specimen in Fig. 50 on the surface of the fragment parting appears to be an unexpanded shoot with unexpanded whorls of branches at each node. Fig. 48 is one of many branch-like fragments about 2 mm wide which are cylindrical and have epidermal cells with bars of thickening (Fig. 49) closely matching those of *E. lyellii* epidermis from elsewhere on the plant.

Other circular bodies with radiating striations (Figs 57–60) are quite different from the nodal diaphragms in having a complete covering of cuticle, and are without doubt the sporangiophores of *E. lyellii*. Some have been removed whole from the matrix using HF and then either macerated or mounted for the SEM. The outer surface seen in Fig. 61 shows that the epidermal cells are of the usual rectangular wavy-walled type and Fig. 60 shows the radiating striations as strong surface ridges. The macerated specimens yielded compact clumps of spores such as that in Fig. 62, presumably representing the contents and shape of a single sporangium. Similar spore masses are common in the fragment partings in association with isolated dispersed spores and occur in many palynological preparations. They are sometimes attached to tissues that suggest the remains of sporangiophores. We have been completely unable to ascertain or even estimate the number of sporangia borne on the under surface of the sporangiophore, which we assume had a central stalk as usual. The fairly featureless spores (Fig. 63) lacking elaters match the probable dispersed spore *Pilasporites allenii* Batten. Attempts have been made to find elaters amongst the spore masses by mounting broken, unmacerated pieces of the sporangiophores but this has so far proved unsuccessful. However, the amount of fragment bed material studied in this







Figs 35–37 *Equisetites lyellii* (Mantell). All × 50. 35, transverse section of cortex showing outer layer with ridged surface, and parenchymatous inner layer with notches into which outer cortex protrudes; V.44949; see also Fig. 34. 36, t.s. showing solid cortex, dark endodermis (arrows) and ring of metaxylem; V.44948. 37, t.s. of specimen showing remains of vallecular canals and small subsidiary traces (arrowed); V.44951.

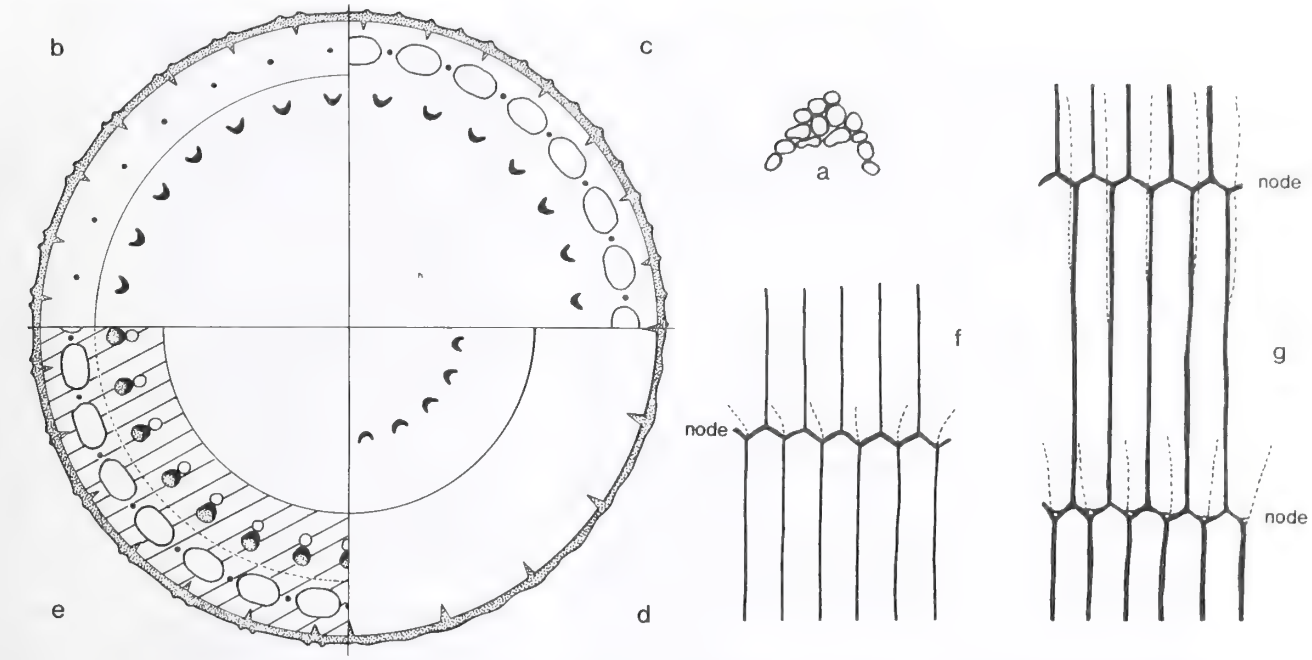


Fig. 38a–e, g *Equisetites lyellii* (Mantell). a, crescent-shaped xylem of a single well-preserved internodal bundle; protoxylem appears intact; V.44951, × 50. b, c, d, diagrammatic transverse sections: b, V.44949; c, V.44953; d, V.44948; e, reconstructed transverse section; all × 15. g, diagram to show suggested form of stele in *E. lyellii*; f, diagram to show form of stele in extant *Equisetum*; both × 10.

way has been relatively limited and extensive searching of newly collected blocks might prove fruitful.

A further type of circular body (Figs 53, 54), with an even, all-over pattern of small perforations in a layer of coalified material, continues to mystify us. The diameter of these spotted bodies is about 2 mm. It seems highly likely that they originate from *E. lyellii* and any suggestions as to their nature would be welcome.

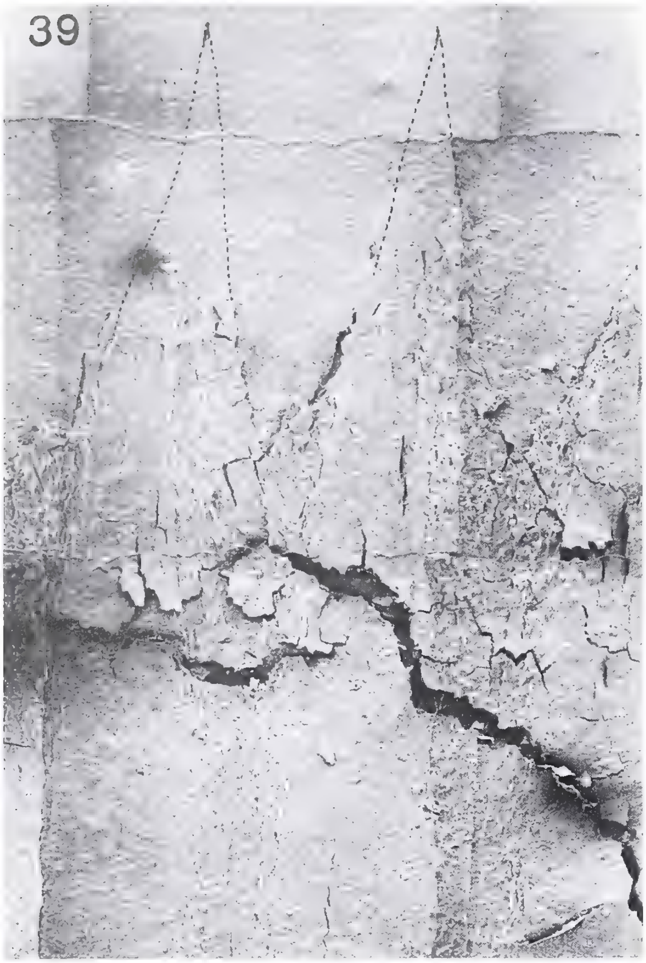
The carbonate nodule with petrified material consists of two separate finds. The first was a single nodule of calcareous mudstone, the whole of which was used to produce, by grinding, a number of longitudinal and transverse sections which were then made into permanent slide mounts. The preservation is imperfect but adds some information about the internal anatomy of *E. lyellii*. The second find of nodular material included the specimen shown in Fig. 29. This is a vertical cut-face showing transverse sections across the hollow rhizomes in growth position. Several such faces have been used to prepare cellulose acetate peels but the preservation of the plant material is less good than that in the permanent mounts. Some of the slides show little or no detail, particularly the longitudinal sections, and the information presented below has been obtained only from the transverse sections. It is certainly possible that the nodule V.63059 (Fig. 29) and others found with it would yield considerably more details of the internal anatomy with further study, but the specimens would have to be sacrificed to further cutting and extensive peeling.

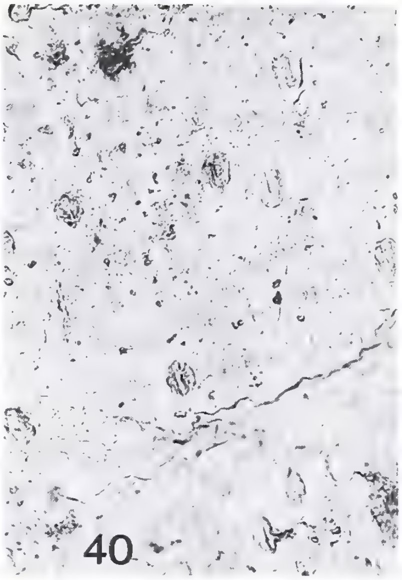
Figure 30 shows the best of the transverse sections, which is obviously from an aerial shoot with a diameter of 7 mm and circular cross section. There is some doubt about whether the other sections represent rhizome or aerial shoot but certain features, such as the ridged and grooved surface (Figs 35, 38) and the number of vascular bundles, point to the latter. The rhizome surface of a living *Equisetum* undulates rather than having a sharply and evenly ridged surface like the aerial shoot of most *Equisetum* species.

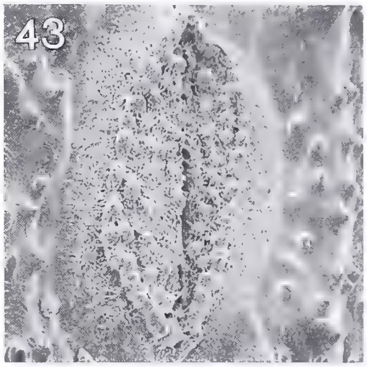
The cortex is composed of two distinct layers; an outer dark, fibrous layer (Figs 31, 35) in which thickened cells are sometimes seen, and a deep inner cortex (Figs 35, 36) of large isodiametric cells with fairly thin walls. The outer cortex is approximately 0·1 mm deep except at a point opposite the vallecular canal where it protrudes into the inner cortex in a wedge shape (Figs 35, 38c). In some slides the inner cortex is solid (Figs 35, 36, 38b) whereas in others the vallecular canals are present in it (Figs 30, 31, 37, 38c). The former are taken to indicate that a parenchymatous diaphragm was present in the nodal region; the latter are internodal sections. In the sections from both regions occur what appear to be small, circular vascular traces in addition to the main vascular bundles (Figs 34, 37, 38b, c). These resistant traces are indicated by arrows in Fig. 37. To the inside of the vallecular canals a strong dark line is sometimes present (arrows in Fig. 36) in the position where one would expect the endodermis. Inside this line the soft tissues are not preserved for more than about two rows of cells (Fig. 36). Thus the xylem of the main bundles is isolated in the middle. Most of the specimens have a ring of 28 or 30 vascular bundles, with only the metaxylem preserved. Each is a crescent or V-shaped mass of about 14 tracheids with the arms pointing to the outside (Figs 32, 35). Occasionally one or two protoxylem elements remain at the point of the V. The xylem is sometimes seen longitudinally (Fig. 33) with either annular or spiral thickenings.

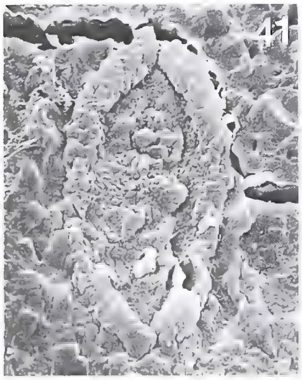
The specimen shown in Figs 36 and 38d is perhaps near a node at the very base of the shoot, or even on the rhizome. It bears an appendage which appears to be a small root with a central vascular strand. It also differs from most other sections in having a much smaller ring of vascular bundles, no vallecular canals and no subsidiary vascular bundles (Fig. 36). Of course close to the node one would expect some indication of the bundles joining to form the nodal ring, but there is no such indication.

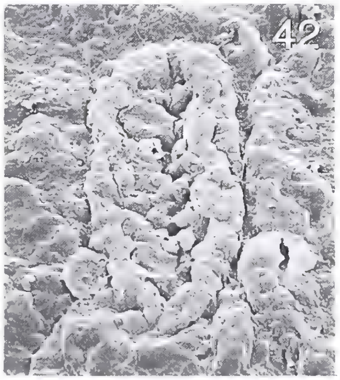
Figure 38b–d comprises diagrams of three specimens in

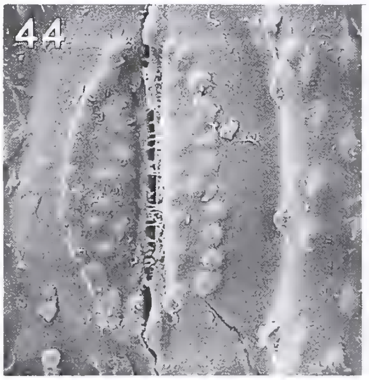












Figs 39–42 *Equisetites lyellii* (Mantell). 39, SEM montage of leaf sheath of aerial shoot showing sculptured cells of the commissures; dotted lines indicate positions of leaf tips broken during preparation; from fragment parting, V.63060, × 50. 40, naturally oxidized piece of internode cuticle from fragment parting showing stomata in broad band, probably internode of aerial shoot from above ground level; V.63076, × 125. 41, 42, two of the stomata (only 5 or 6 were found) from specimen in Fig. 39; × 1000.

Figs 43–44 *Equisetum sylvaticum* Linnaeus. Internode stomata of living species, showing silicified surface closely resembling *E. lyellii*; × 1000.

transverse section, and a reconstructed section which is mostly based on the available information, but has added features which are purely conjectural. The exact position of the surface ridges is not clear as it appears to vary, but the arrangement in slide V.44949 (Fig. 35) is taken as typical. It should be pointed out that in living species of *Equisetum* the surface ridges are on the same radii as the vascular bundles. In none of the sections have we been able to identify the leaf-sheath surrounding the stem. One should consider the possibility that the layer we have identified as outer cortex might in fact be the leaf sheath very closely pressed into the contours of the stem surface. This interpretation would produce sharply defined shallow notches separating broad, flat ridges opposite the vascular bundles.

Discussion. One of the outstanding differences from modern horsetails is the large amount of metaxylem in *E. lyellii*, but an even more anomalous feature is the presence of the ring of small vascular traces which, as far as we can tell, are between the vallecular canals (Fig. 37) and on the same radii as the main vascular bundles. The normal arrangement of the vascular tissue in extant *Equisetum* is shown in Fig. 38f, but there is some disagreement about the exact nature of such a stele. The various viewpoints which revolve around whether the internodal bundle is a composite structure or a single unit have been summarized with great clarity by Parihar (1965). In general terms the internodal bundles may be considered to trifurcate at the node with the median strand passing out as a leaf trace. The lateral strands diverge to the left and right and unite with adjacent strands to form the alternating ring of bundles in the next internode above. In this process of splitting and reuniting, which is condensed at the node, a continuous ring of xylem is produced. The evidence we have for *E. lyellii* indicates that the vascular arrangement at the node was very similar to that in extant *Equisetum*. We know that the vascular bundles of *E. lyellii* normally alternate in successive internodes, but not invariably. Specimen V.51137 (Figs 21, 22), which is an internal mould of the hollow rhizome with ferruginous impressions of the vascular bundles, shows this non-alternation in several places. This specimen is also of special interest in apparently displaying leaf-gaps at some of its nodes (Fig. 22). The presence of leaf-gaps in living *Equisetum* is a little-known feature described originally by Browne (1939) and later in detail by Moore (1941) from several species. We also know that the whorls of leaves usually alternate at successive nodes, and although we cannot actually demonstrate that the leaves alternate with the bundles of the internodes above, the position of the probable leaf gaps (Figs 21, 22) strongly supports this. Assuming it to be so, we can only account for the small bundles by suggesting that they are leaf traces which depart from the main bundle at some distance below the node (Fig. 39g). They would thus be on the same radius as the bundle from which they arise and also the leaf above into which they would pass as the leaf trace. On the other hand the presence of the small leaf gaps seems to us at variance with this arrangement, since we assume the traces would diverge into the leaves without further disturbance to the main vascular bundles. However, we are working at the very limits of the material and at this stage we can only speculate that such anomalous leaf departure was not universally present. Alvin & Hluštik (1979) have demonstrated a similar situation in the Lower Cretaceous cheirolepidiaceous conifer *Frenelopsis alata* (K. Feistmantel), where the steles of side branches sometimes depart from below the node.

From the above evidence it is clear that the anatomical features of *E. lyellii* are rather further removed from the modern genus *Equisetum* than the external morphology suggests, and it is in the light of this that we prefer to retain it in the genus *Equisetites* Sternberg.

Amongst modern botanists there are still differences of opinion concerning the status of the genus *Equisetum* and its subdivisions. Here we need not consider more than the two major sub-groups, subgenus *Equisetum* and subgenus *Hippochaete*, which are easily distinguishable (see Page 1972*a*, 1974). The main features of the former, commonly called the horsetails, have been listed above under the discussion of *Equisetum burchardtii*. To these details it may be added that the stomata occur in a broad scattered band along each furrow of the stem. The stomatal cells are level with the surface and covered in a microscopic ornamentation of silicified beading, as in the stomata of *Equisetum sylvaticum* shown in Figs 43 and 44.

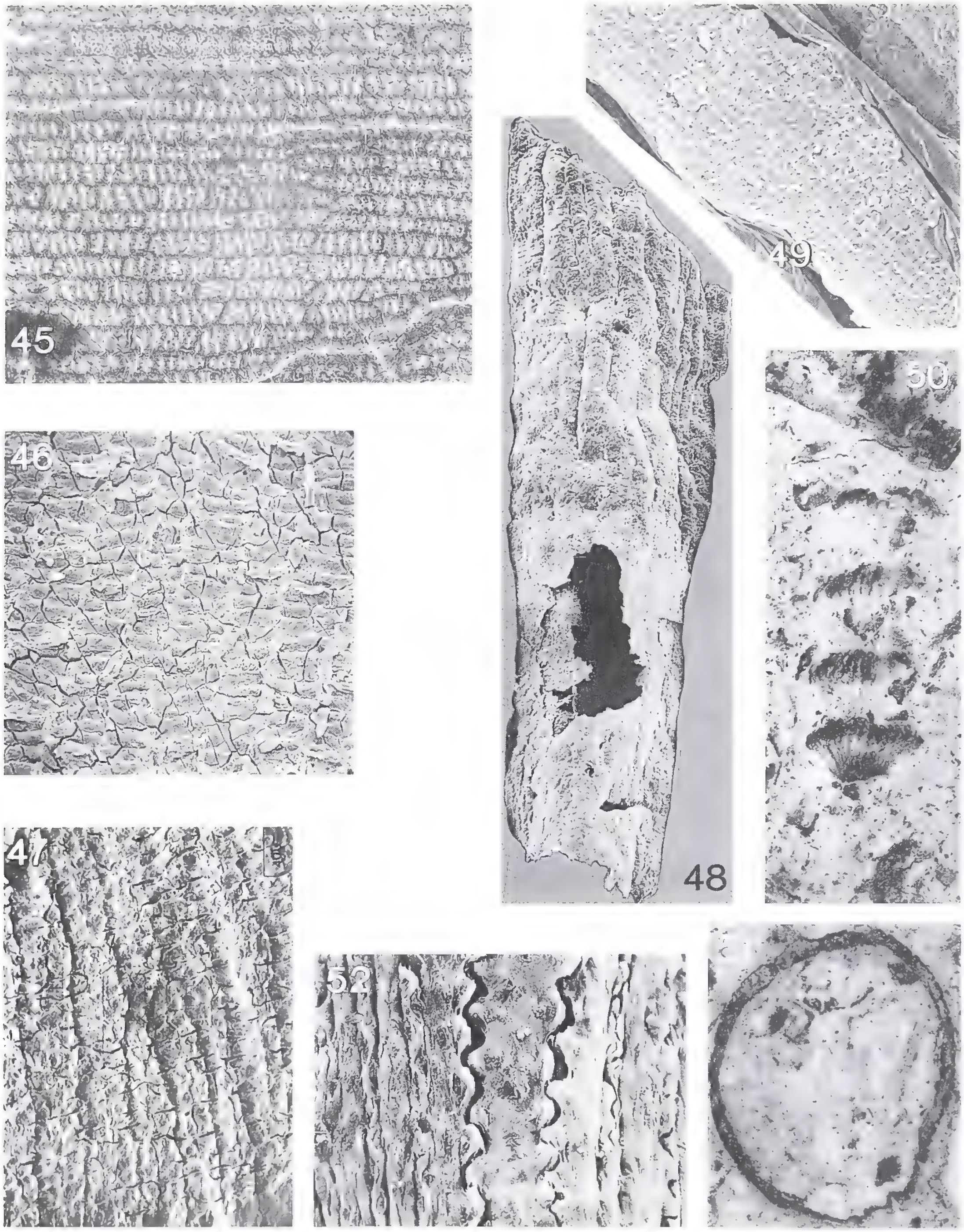
Members of the genus *Equisetum* subgenus *Hippochaete*, commonly known as the scouring rushes, are characterized by having hard, winter-green shoots which persist for up to three years. The rhizome has a large central canal and is never found with tubers. The aerial shoot has a relatively large number of leaves per node and the branches resemble the main shoot in being rounded and hollow. The stomata are arranged in one or two regular longitudinal files along the stem and are sunken in crater-like pits. The stomatal cells are non-beaded but there is coarse silica thickening around the rim of the crater (see Page 1972*a*).

It is quite obvious that *E. lyellii*, whilst displaying many of the features of the subgenus *Hippochaete* in its gross morphology, has stomata which both in distribution and structure are entirely typical of the subgenus *Equisetum*. Page (personal communication) considers that it should be regarded as at least subgenerically distinct from the two groups of modern species, i.e. as representing a now extinct third subgenus. Preliminary studies of the stomata of several Jurassic and Triassic species suggest that this subgenus may have been worldwide in the Mesozoic; see Page (1972*b*, 1974) for discussion of evolutionary evidence within the Equisetales and older articulates.

Suggested anatomical and morphological reconstructions of *Equisetites lyellii* are presented in Figs 38e and 67 respectively. The reconstructed transverse section of the aerial shoot internode (Fig. 38e) includes phloem and carinal canals which form in extant species by breakdown of the protoxylem during elongation. It seems reasonable to suppose that phloem was present between the arms of the crescent of metaxylem. The question of carinal canals is less clear as the presence of protoxylem elements in some of the bundles could be taken as an indication that these canals were absent.

The suggested reconstruction of *E. lyellii* (Fig. 67) is based on the new information given above, together with all the detailed measurements and field observations given by Allen (1941), though of necessity several features have been included for which there is absolutely no evidence. As with the reconstruction of *E. burchardtii* the choice between suggesting monomorphic or dimorphic habit was fairly, though not entirely, arbitrary. All extant members of the subgenus *Hippochaete* have only one kind of shoot but on balance we favour a dimorphic habit for *E. lyellii* for two reasons. The paucity of branches on aerial shoots in the fragment beds observed by Allen in the field (1941) must mean that many of the shoots were unbranched. The lack of a complete fertile cone but the relative abundance of isolated sporangiophores suggests that this part of the plant decayed rapidly on reaching maturity. One should also note that the sporangiophore heads of *E. lyellii* are rounded in shape, unlike modern species in which they become pentagonal as the result of close-packing. This further suggests a less robust structure, and we thus opt for the attractive notion of long, pale, fertile shoots bearing their delicate cones above the water, shedding their spores and soon becoming fragmented.

Comparison. Because of the exceptional material available for study this species is now known in more detail than any other Mesozoic member of the family. This makes useful comparisons even more difficult than before. The name

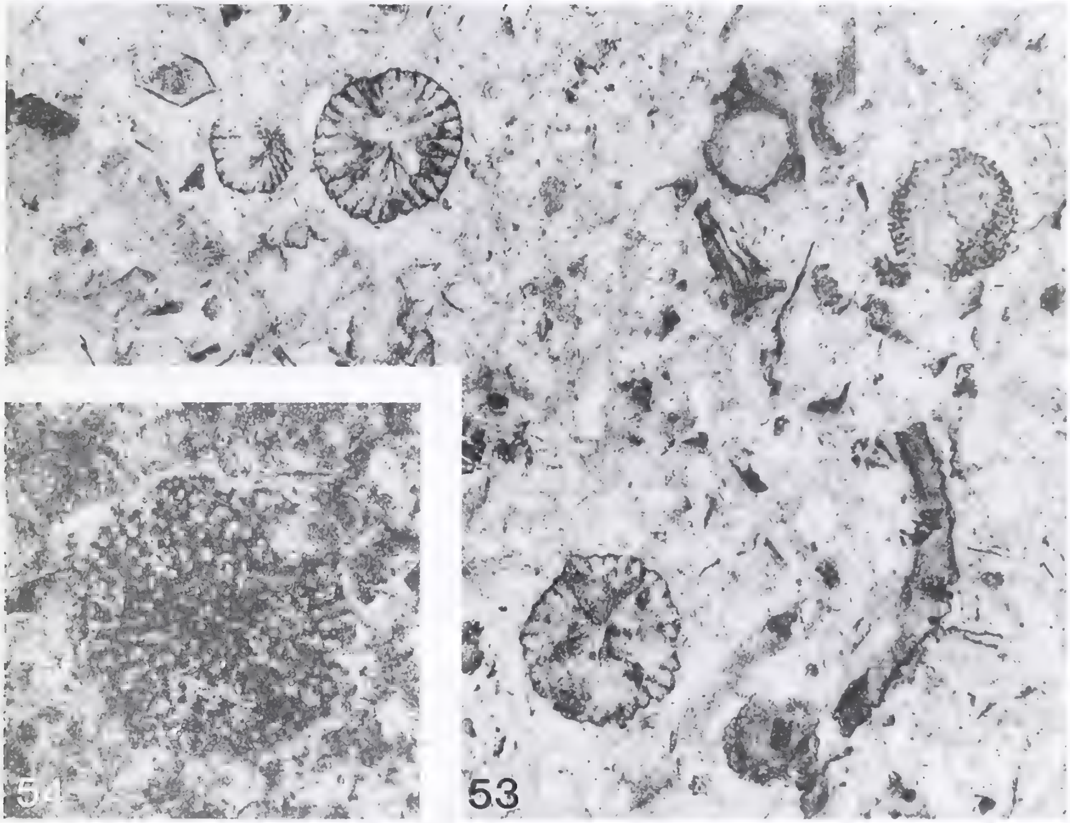


Figs 45–51 *Equisetites lyellii* (Mantell). All specimens from fragment beds. 45, rhizome cuticle naturally oxidized, showing transverse bars of thickening on cells; V.63075, × 100. 46, 47, similar pieces of cuticle in SEM; 46, inner surface, V.63060, × 250; 47, outer surface, V.63062, × 250. 48, small cylinder of cuticle presumed to be a branch borne by aerial shoot; V.63063, × 25. 49, piece of cuticle broken from middle of specimen in Fig. 48, in SEM showing cells matching those of rhizome (Figs 45, 46); × 100. 50, probable unexpanded shoot apparently with whorls of branches; V.63967, × 8. 51, hollow shoot broken off at surface of fragment bed; V.63064, × 10.

Fig. 52 *Equisetum telmateia* Ehrhart. Desilicified internode in living species, revealing elongate, sinuous cells similar to those of *E. lyellii*; × 1000.

Equisetites lyellii (Mantell) has been given to Lower Cretaceous equisetalean material from a number of countries worldwide, but at this stage it is impossible to assess the validity of these determinations. Some of them, such as the material from the Potomac Formation, U.S.A. (Fontaine 1889), are probably identical but new specimens are essential for study as Fontaine's originals are missing from the Smithsonian Institution.

The only other material known in comparable detail is that described by Gould (1968) from the Jurassic of Australia.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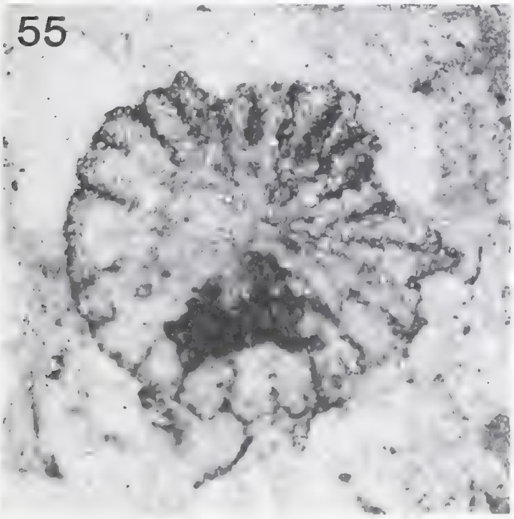
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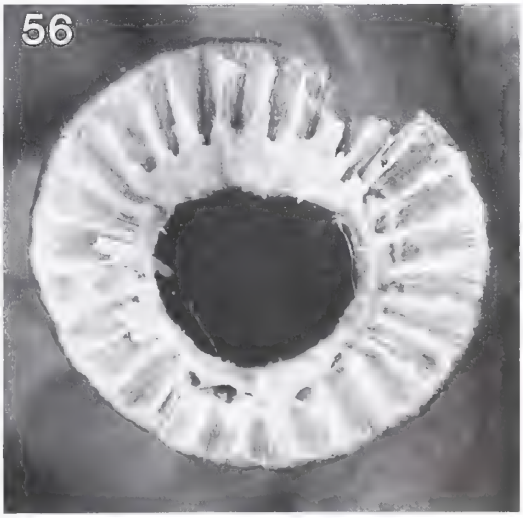
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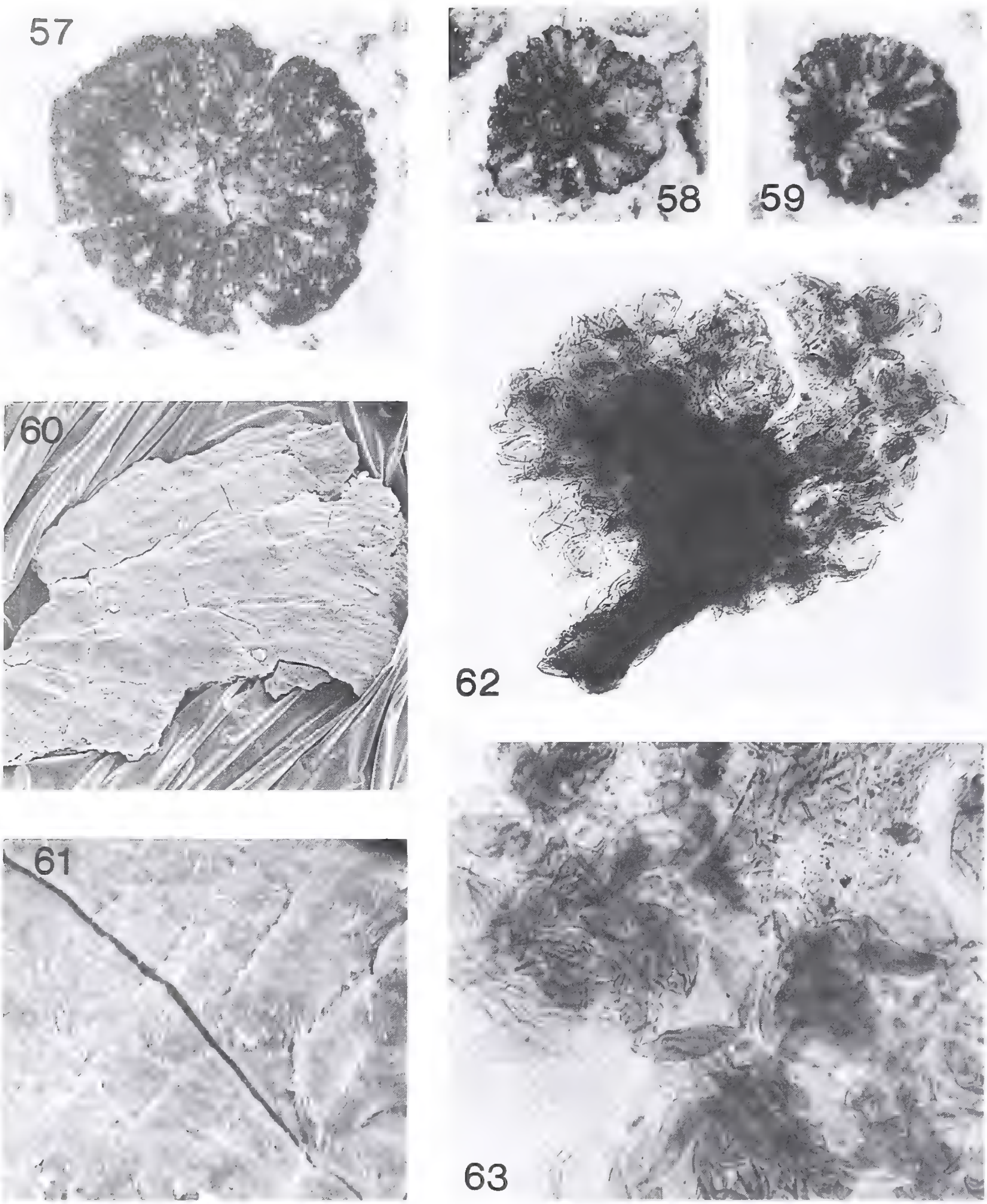
Figs 53–55 *Equisetites lyellii* (Mantell). 53, typical surface of fragment bed photographed under paraffin showing nodal diaphragms etc.; V.63064, × 10. 54, spotted disc of type very common in fragment bed, derivation unknown; V.63069, × 20. 55, nodal diaphragm; V.63064, × 20.

Fig. 56 *Equisetum telmateia* Ehrhart. 'Nodal diaphragm'; see p. 47 for discussion; × 8.



Figs 57–63 *Equisetites lyellii* (Mantell). 57–59, sporangiophore heads showing radiating ridges on outer surface; 57, V.63067; 58, V.63064; 59, V.63068; all × 20. 60, unmacerated portion of sporangiophore head in SEM, curved edge on right, surface ridges radiating from broken central point on left (background, heat-damaged sellotape); V.63065, × 100. 61, surface of same specimen showing cells with undulating walls very similar to rhizome cuticle; × 500. 62, 63, spore mass obtained by macerating sporangiophore head, presumed to be contents of a single sporangium, V.63066; 59, × 225; 60, × 700.

There are two species, *Equisetum laterale* Phillips and *Equisetum bryanii* Gould. Both are similar to *E. lyellii* in having scattered stomata and sinuous-walled epidermal cells with bars of thickening. It would be interesting to study this material again along with other Mesozoic species in the light of the phylogenetic considerations raised by the subgeneric status of *E. lyellii*.

SPORAE DISPERSAE

Genus *PILASPORITES* Balme & Hennelly

For remarks on *Pilasporites* see Batten, 1968.

Pilasporites allenii Batten Figs 64–66

1968 *Pilasporites allenii* Batten: 638, pl.123, figs 1–4, 6, 10–14.

DESCRIPTION. For the diagnosis and fully illustrated account of this species see Batten's (1968) original description. Figs 64–66, p. 56, are representative photomicrographs of these isolated dispersed spores.

The spores of *Pilasporites allenii* were spherical or subspherical in shape before being compressed in sediment. They consist of a comparatively thick exine (exospore) surrounded by a flimsy, crumpled, closely adhering perine (perispore) which commonly bears a surface deposit of scattered granules. Despite its fragile appearance the outer membrane is clearly tough and resistant to chemical treatment, including oxidation. The exine is unornamented and devoid of a trilete or monolete aperture (Figs 63–65). In these respects the spores are entirely comparable to those of extant *Equisetum* (see for example Gullvåg 1968, Lugardon 1970, Guervin *et al.* 1972, Good 1975, Tryon & Tryon 1982, Kurmann & Taylor 1984).

Despite the alete appearance, a darkened patch is displayed on some specimens (Figs 64, 65) which resembles the 'stopper' found by Lugardon (1970) in the wall of spores of extant *Equisetum maximum*, but its diameter is more than three times as great. In this respect it suggests a closer relationship to the proximal area of geologically older spores with diminutive triradiate marks that are referred to *Calamospora*. If it did function as an operculum, which is unlikely, then the mode of germination of the spores of Cretaceous *Equisetites* may have varied, because others clearly had a tendency to split, as commonly seen in acetolysed products of extant species. Where opened in this way the exine along the margins is often slightly folded inwards.

DISCUSSION. Acetolysis, a chemical method frequently used for preparing modern and Quaternary palynomorphs for examination by transmitted light microscopy, is known to dissolve the elaters of extant *Equisetum* spores which, when coiled, envelop the perispore. No Wealden specimens have yet been found with these extra-perinous elements. The possibility that they were removed during sediment diagenesis or by chemical treatment of rock samples in the laboratory has been mentioned previously by Batten (1968). He also suggested that they might not have had them in the first place. Similar spores were reported by Gould (1968) from cones of the Australian Jurassic species identified as *E. laterale* Phillips. These also lack elaters, as do specimens isolated much earlier by Halle (1908) from compressions of *Equisetites* and those encountered in cones found more recently by Vozenin-Serra & Laroche (1974, 1976).

The pre-Quaternary fossil record of vascular plant spores with elaters is limited to associations with some Carboniferous calamites (Wilson 1943, 1963, Baxter & Leisman 1967, Good & Taylor 1974, 1975, Good 1975, 1977) and with two equisetaleans, from the Middle Jurassic (Harris 1978) and early Tertiary (Chandler 1964). Sphenophyllalean products are quite different (Taylor 1986). The calamite spores are trilete with three distally attached elaters; they are not closely similar to those of modern *Equisetum*, which are alete and have four elaters. They are thought likely to represent the most mature and best preserved specimens, whereas contemporaneous cones that yield spores lacking elaters are considered to be immature (Good 1975, 1977). Although a triradiate mark is typically present on calamite spores (Hartung 1933) its presence does not necessarily distinguish them from those of the Equisetaceae. Both Carboniferous and early Mesozoic equisetalean species have yielded spores of similar character (see for example Halle 1908 and Gastaldo 1981).

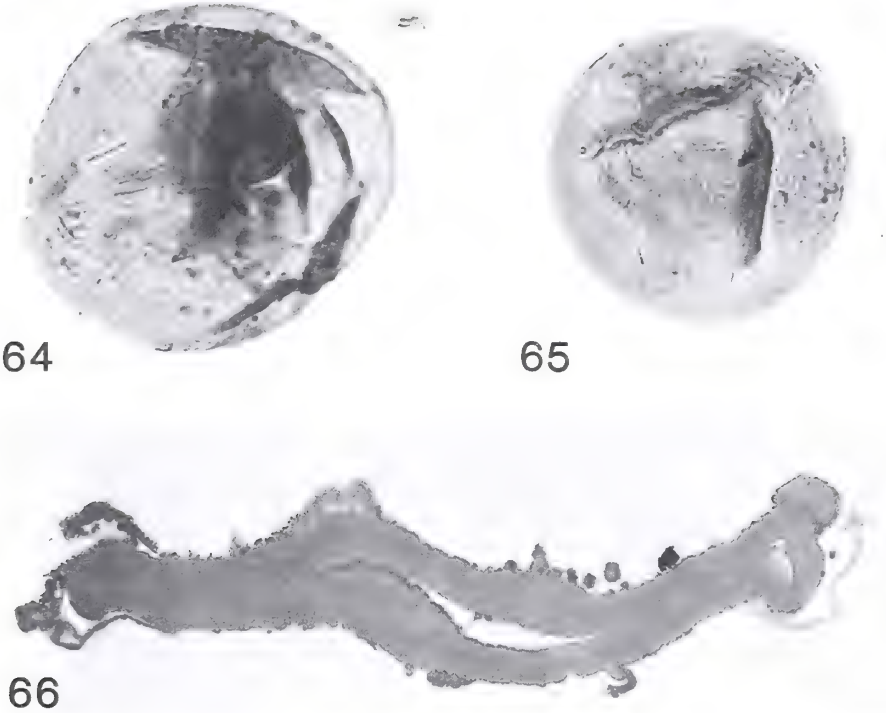
Harris (1978) found some round palynomorphs in rock matrix between sporangiophore heads of *Equisetum columnare* which seemed to bear fine threads resembling elaters. But he was not sure that they were produced by *E. columnare*, and he also noted that the threads visible on the two specimens he illustrated (Harris 1978: text-fig. 2D) were incomplete. By contrast the early Tertiary spores recovered from an *Equisetum* cone by Chandler (1964: plate 1, figs 3, 4) are remarkably similar to extant forms.

Did the spores of *Equisetites lyellii* bear elaters? If they did then surely one should find them preserved within the spore masses? Those remains of broken and decayed fertile cones which have been isolated from fragment partings without chemical treatment have so far failed to reveal any. Is this because they were immature at the time they were deposited (cf. Good 1975)? Hence, is the absence of elaters on specimens in masses a function of developmental factors, and on single and presumed fully mature spores because they decayed rapidly after dispersal? Or has the search proved fruitless because they were never developed? Species of *Equisetum* which produced elater-less spores could represent part of an extinct taxonomic grouping within the Equisetaceae, as suggested already on the basis of the morphology and anatomy of *E. lyellii*.

COMPARISON. Batten (1968, 1973) compared *Pilasporites allenii* with a number of dispersed miospores that had been referred previously to the Equisetaceae and with morphologically similar species which had not been linked to this family. Several additional records that fall into one or other of these categories are considered below.

Maljavkina (1956) referred triradiate spores she recovered from the Cretaceous of the eastern Gobi depression to a new, but invalid and superfluous, genus *Equisetacites*. Alete species included in different genera erected earlier by the same author (Maljavkina 1949) have also been linked by some Soviet palynologists to *Equisetites* or the Equisetaceae. Vinogradova (1971) described as new a palynomorph from the Jurassic of Mangyshlak and western Turkmenia which she named *Equisetites variabilis* (see also Bolkhovitina & Fokina 1971). McKellar (1974) erected *Peroaletes rugosus* for Jurassic spores from the Surat Basin of Australia; these appear to be similar to *Pilasporites allenii* but have a more rigid exine and lack the dark patch seen on some Wealden forms.

Burger (1976) identified *Concentrisporites hallei* (Nilsson) Wall from the Lower Cretaceous of the Great Artesian Basin of Queensland, Australia. This species was originally reported (as *Equisetosporites hallei*) from Rhaetian and early Jurassic rocks of Sweden and considered closely comparable to, if not identical with, the spores of *Equisetites* (*Equisetostachys*) *suecicus* (Nathorst) Halle (see Nilsson 1958: 66–67 and Batten 1968: 241). Similar, indeed probably identical, forms have been recorded from the Jurassic of France (Danzé-Corsin & Laveine 1963), Canada (Pocock 1970, referred to *Concentrisporites pseudosulcatus* (Danzé-Corsin & Laveine) Pocock) and Australia (Reiser & Williams 1969, identified as *Perinopollenites elatoides* Couper). More recently Taugourdeau-Lantz & Dubois (1979) described as new *Pilasporites petri* and *P. calabrensis* from the Middle Jurassic of Calabria, Italy. Both were considered to have probable equisetalean origins, whereas the spores referred to ?*Equisetum* by Mamczar (1986) are unlikely to have any connection with this group. Finally, a scanning electron micrograph of the surface of an inaperturate palynomorph, thought by



Figs 64–66 *Pilasporites allenii* Batten, the probable dispersed spore of *Equisetites lyellii* (Mantell). 64, 65, V.63073, × 1000. 64, spore showing subcircular patch of thickened exine and scattered granules on closely-adhering perine. 65, typical specimen of *P. allenii* with membranous perine closely enveloping and crumpled against the exine. 66, cross section of spore showing thick, homogeneous exine surrounded by a thin perine bearing scattered granular bodies; V.63074, × 4000.

Kedves (1979) to have possible algal origins and identified as *Psophosphaera intrapunctata* (Kedves) Kedves, displays the sort of crumpling and scattered granular bodies that characterize the perine of *Pilasporites allenii* (compare Batten 1973: pl. 42, figs 10, 11 with Kedves 1979: pl. 3, fig. 1). None of these palynomorphs is, however, unequivocally identical with the Wealden spores.

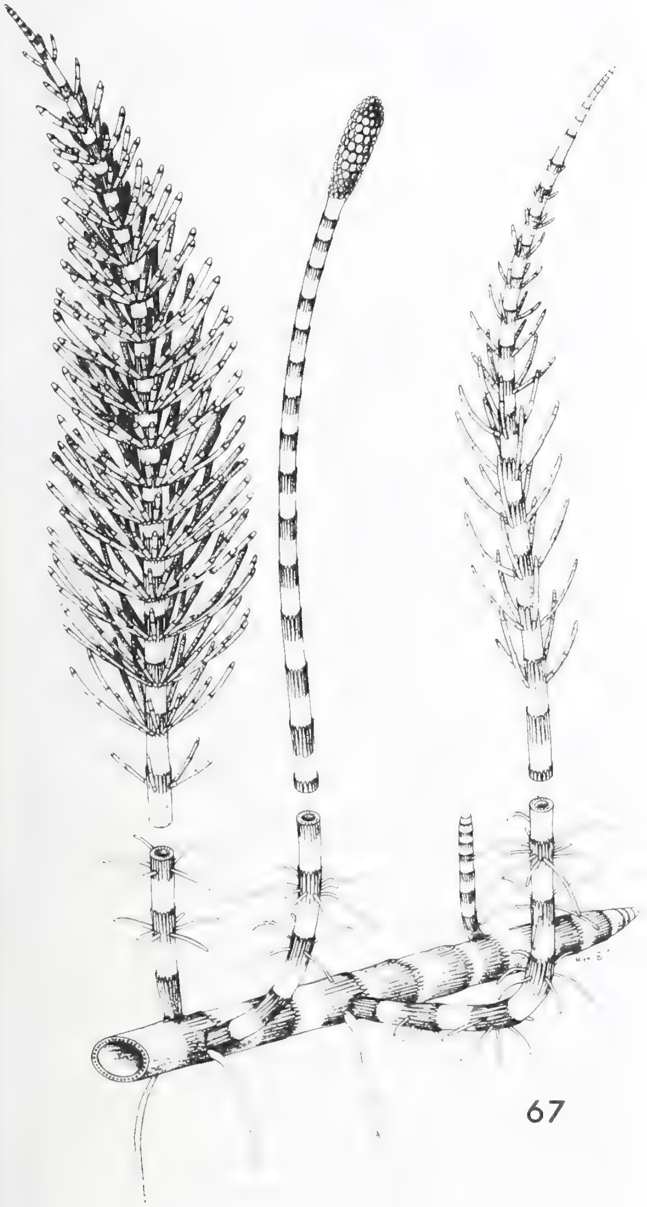
PALAEOENVIRONMENTAL SIGNIFICANCE

Where *Equisetites lyellii* is preserved in position of growth it is typically associated with thinly interbedded mudstones and siltstones. The latter commonly occur in lenticular units within the finer-grained deposits, forming the 'passage beds' of Allen (1959, 1976). These are subaqueous sedimentary accumulations and, although conveniently referred to as 'soil beds' for descriptive purposes, are generally not regarded as palaeosols *sensu stricto*. Allen, however, regards them as fossil aquatic soils at the 'wet end' of a continuous spectrum of soils, all supporting plants, from totally wet through reed-swamp and marsh to subaerial (1976 and personal communication). Well stratified weathering profiles indicating subaerial soils have been confirmed in the Wealden of northern France (Meyer 1976), but only suspected in southern England (Lake & Thurrell 1974, Allen 1976, 1981, Stewart 1981) where high rates of deposition and frequent erosion appear to have hindered their development. Red-mottled silts and clays with traces of roots in growth position and indications of iron-pan development in places imply fluctuating water tables, soil-forming alterations and local leaching, but exposure does not seem to have been long enough for weathering to have completed the pedogenic process.

All the *Equisetites lyellii* soil beds were probably under water to a depth of up to 0·5 m, if not permanently then at least more often than not. Possibly the plants could have withstood total immersion for short periods. The presence of only a few widely scattered stomata on the lower parts of the stems supports an aquatic habitat. By contrast, *Equisetum burchardtii* may have grown in better-drained sediment more often exposed or above the water table. This is suggested by its occurrence in sandier facies and by the presence of tubers on the rhizomes of the plant. In extant species of *Equisetum*, these are formed and consumed on a seasonal basis but it is possible that in *E. burchardtii* this happened in response to alternating wet and dry periods. Seasons need not be invoked. Tubers characterize only those members of the subgenus *Equisetum* which grow on dry land and have deciduous aerial parts. It follows, therefore, that the Wealden species was probably a herbaceous perennial which might well have died when its habitat became swampy or permanently flooded.

For *Equisetites lyellii* the combination of a subtropical climate and the preferred habitat being standing water suggests that, despite fluctuations in rainfall (Allen 1976, 1981, Sladen & Batten 1984), die-back occurred only sporadically during periods of drought and was not an annual event. This is consistent with the 'winter-green' interpretation of the species suggested and discussed here.

The plants are visualized as occupying extensive areas of the watery late Purbeck and Wadhurst mud-plains where



67

Fig. 67 A suggested reconstruction of *Equisetites lyellii* (Mantell) as discussed in the text. Approximately × ½. © Joan Watson, 1990.

deposition took place slowly in quiet conditions. Some (e.g. the Brede Soil Bed) were clearly 'reed-swamp' communities fringing the shores of lakes and bays (Allen 1959). The rhizomatous system of growth enabled communities not only to spread rapidly and keep pace with changes in water depth but also prevented mud from smothering them by keeping up with sedimentation. The scattered occurrences of *E. lyellii* in other Wealden deposits (e.g. the Grinstead Clay) and the tendency for their stems and rhizomes to be more slender may reflect a response to conditions that were less conducive to colonization and vigorous growth. These probably included slightly raised salinities.

The arenaceous units of the Wealden succession, whether interpreted as mainly representing sandy braidplains (Allen 1976, 1977, 1981) or, as previously invoked, deltaic accumulations on a large or small scale (e.g. Allen 1959, 1962, 1976, 1977, Lake 1977, Worssam 1977), were clearly inhospitable to *Equisetites* and *Equisetum*. Recent work on the distribution of dinoflagellate cysts and other algae (Batten 1982, 1985 and in preparation; Harding 1986) suggests that the Wadhurst waters were generally fresher than those of Grinstead and Weald Clay times. This could account for the scarcity of equisetalean remains in the younger formations which otherwise represent deposition in broadly similar mud-plain conditions. It could also confirm earlier suggestions (e.g. Allen 1959, Allen *et al.* 1973, Batten 1968, 1975, 1977) that the plants grew only where the water was usually fresh and hence provide an answer to the question—what killed off the established communities?

It is difficult to follow their upward development. Erect stems are commonly terminated by fragment partings, which suggests that the plants were destroyed catastrophically. Although it is possible that they could have been overwhelmed by a sudden influx of a large amount of sediment, there is generally no evidence for this. Even if it could be demonstrated, attempts by the plants to grow up through the overburden would surely be preserved. Allen (1938, 1959) found some evidence for this but it has not been proved beyond doubt. Rhizomes of modern *Equisetum* are able to grow upwards and continue above ground as aerial stems and have been found as much as fifteen feet (4·5 m) below ground in an evenly soft substrate, attached to the upper layers by thin vertical rhizomes. The fragment partings may indicate physical damage to communities (Allen 1947, 1959, Batten 1968) or sometimes merely consist of partly decomposed litter of old stems. Total destruction is not necessarily implied. Nevertheless this did take place, and the prime cause is likely to have been inundation with saline water. Complete immersion by fresh water for an extended period (years rather than months) is also a possibility. The former interpretation is supported by evidence from the ostracod and molluscan assemblages (e.g. Allen 1959, 1976, Allen *et al.* 1973, Anderson *et al.* 1967) and phytoplankton (Batten in preparation) recovered from beds that lack *E. lyellii*. Once the plants had died the stems broke off and sediment dropped into the hollow open ends, thus enhancing their chances of being preserved *in situ*.

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APPENDIX: STRATIGRAPHIC OCCURRENCES

Details of specimens figured in this paper and other notable material not figured here.

Figure	Collection	Spec.No.	Locality	Horizon	Comments
Equisetum burchardtii					
1, 2, 3	Humboldt	57	Harrel bei Bückeburg	Berriasian	Neotype. Figd Watson 1983: pl.13, fig.1
4	,,	6	,,	,,	Figd Watson 1983: pl. 13, fig. 2
5, 6, 7, 8	,,	7	,,	,,	
9	B.M.(N.H.)	V.1070	Prob. Ecclesbourne, nr Hastings, E. Sussex	?Ashdown Beds	Figd Watson 1983: pl. 13, fig. 3
10	Humboldt	88	Harrel bei Bückeburg	Berriasian	Figd Schenk 1871: pl. 30, fig. 1
11	,,	87	,,	,,	
12	,,	85	,,	,,	
unfigured	B.M.(N.H.)	V.1070a	Ecclesbourne, E. Sussex	?Ashdown Beds	
,,	,,	V.2730b	,,	,,	Rufford Colln.
,,	Humboldt	1984/745	Harrel bei Bückeburg	Berriasian	Nice erect stems.
Equisetites yokoyamae					
13	B.M.(N.H.)	V.2335	Ecclesbourne, E. Sussex	?Ashdown Beds	Figd Seward 1894: fig. 3 (with incorrect specimen number) and fig. 3*
unfigured	,,	V.2834	Bexhill, E. Sussex	,,	Very small tubers and thin rhizomes discussed in text, p. 42.
Equisetites lyellii					
15	Sedgwick	K.2221	Brede, E. Sussex	Wadhurst Clay, Brede Soil Bed	Figd Allen 1941: pl. 24A; Watson 1983: pl. 13, fig. 4.
16	B.M.(N.H.)	3605	Poundsford, E. Sussex	top Purbeck	Lectotype. Figd Mantell 1833: 245, fig. 3.
17	,,	39123	,,	,,	Figd Mantell 1833: 245, fig. 2.
18, 27	,,	V.710	St Leonards, E. Sussex	Ashdown Beds	Very well preserved epidermis.
19	,,	V.59	,,	,,	Figd Seward 1894: pl. 1, fig. 4.

Figure	Collection	Spec.No.	Locality	Horizon	Comments
Equisetites lyellii, cont.					
20	B.M.(N.H.)	V.45457	SE Ashurst Wood, E. Grinstead, W. Sussex TQ 412367	Wadhurst Clay, Balcombe Soil Bed	Coll. C.H. Shute & P. J. Whybrow.
21, 22	,,	V.51137	,,	,,	Thickest known rhizome.
23	Sedgwick	K.2139	Baldslow Wood, Westfield, E. Sussex.	Wadhurst Clay, Brede Soil Bed	Figd Allen 1947: fig. 57A.
24	B.M.(N.H.)	V.63058	East Grinstead, W. Sussex. TQ 377387	Wadhurst Clay, High Brooms Soil Bed	Coll. C. H. Shute
25, 26, 28	,,	26a, V.63070 26b, V.28643 26c, V.63071 26d, V.63072	High Brooms Brick & Tile Co. pit, Nr Tunbridge Wells, Kent. TQ 417594	Wadhurst Clay, High Brooms Soil Bed	Coll. J. E. Owen
29	,,	V.63059	¼ mile S of Ashurst Wood, W. Sussex TQ 419364	Wadhurst Clay, High Brooms Soil Bed	Coll. C. H. Shute & P.J. Whybrow.
30–38 + other unfigd specs.	,,	V.44948 *et seqq.*, see Figs	,,	,,	Coll. P. J. Whybrow. Slides made from nodule.
39, 41, 42	,,	V.63060	Cuckfield No. 1 Borehole	Wadhurst Clay	42 figd Watson 1983: pl. 14, fig. 12
40	,,	V.63076	Danehill, W. Sussex TQ 382266	,,	Figd Watson 1983: pl. 14, fig. 11
45	,,	V.63075	,,	,,	Figd Watson 1983: pl. 14, fig. 2
46	,,	V.63060	Cuckfield No. 1 Borehole	,,	Figd Watson 1983: pl. 14, fig. 3
47	,,	V.63062	,,	,,	
48, 49	,,	V.63063	,,	,,	
50, 57	,,	V.63067	East Grinstead, W. Sussex. TQ 377387	Wadhurst Clay, frag. parting above High Brooms Soil Bed	50 figd Watson 1983: pl. 14, fig. 4
51, 53, 55, 58	,,	V.63064	,,	,,	53 figd Watson 1983: pl. 14, fig. 5.
54	,,	V.63069	,,	,,	
59	,,	V.63068	,,	,,	Figd Watson 1983: pl. 14, fig. 6.
60, 61	,,	V.63065	Cuckfield No. 1 Borehole	Wadhurst Clay	61 figd Watson 1983: pl. 14, fig. 9.
62, 63	,,	V.63066	,,	,,	63 figd Watson 1983: pl. 14, fig. 10.
64, 65	,,	V.63073	Danehill, W. Sussex	,,	
66	,,	V.63074	,,	,,	
unfigured	,,	3599	prob. Poundsford, E. Sussex	? top Purbeck	Mantell Colln. Rhizomes perfectly circular in cross section
..	,,	38375	,,	,,	,,
..	,,	10837	,,	,,	,,
..	,,	38375	,,	,,	,,
..	,,	V.60511	SE Ashurst Wood, W. Sussex	Wadhurst Clay	Longest rhizome spec. in Museum collns, 23 cm long with 16 internodes.

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Cretaceous Bryozoa from the Faringdon Sponge Gravel (Aptian) of Oxfordshire

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SYNOPSIS. The rich bryozoan fauna of the Faringdon Sponge Gravel is the most diverse known from the Aptian. Forty-nine species of cyclostome bryozoans and one species of cheilostome bryozoan are described in this systematic account, which revises the work of Canu & Bassler (1926), making extensive use of SEM to study type and other specimens. The following taxa are described for the first time: *Proboscinopora* gen. nov. (type species *Proboscina divisi* Vine), *Paracrescis* gen. nov. (type species *Paracrescis boardmani* sp. nov.), *'Stomatopora' melvillei* sp. nov., *Stomatoporina alternata* sp. nov., *Filisparsa gasteri* sp. nov., *Collapora hillmeri* sp. nov., *Hyporosopora constricta* sp. nov., *H. larwoodi* sp. nov., *H. mantelli* sp. nov., *Tholopora dightoni* sp. nov., and *T. hastingsae* sp. nov. A dichotomous key is given to assist species identification. Remarks are made concerning generic concepts and ranges of genera. A type species is designated for the genus *Reptomulticava* d'Orbigny, 1854.

Lectotypes are selected for the following species: *Ceata granulata* (Canu & Bassler), *Clausa zonifera* Canu & Bassler, *Entalophoroecia quadripartita* (Canu & Bassler), *Heteropora keepingi* Gregory, *Laterocavea intermedia* Canu & Bassler, *Meliceritites cunningtoni* (Gregory), *M. transversa* Canu & Bassler, *Petalopora cunningtoni* Gregory, *Plagioecia spissa* (Gregory), *Reptoclausa hagenowi* (Sharpe), and *Tetrocycloecia multiporosa* Canu & Bassler.

Aspects of bryozoan palaeoecology and preservation are discussed. A wide range of colony-forms occurs at Faringdon. Arborescent colonies with narrow cylindrical branches dominate, but more robust erect forms are also present, and encrusting colony-forms abound on sponge, shell and pebble substrates. Foliaceous colony-forms are notable for their extreme rarity. The richness of the bryozoan fauna suggests episodic sedimentation in an environment well provided with nutrient-laden currents, possibly at water depths of 100 m or more. Varying amounts of abrasion of fragmented colonies occurred prior to burial. Whereas some specimens are in pristine condition, diagenetic overgrowths of calcite obscures surface details in others.

The Faringdon bryozoan fauna contains a few species in common with faunas of similar age from south-eastern France and western Switzerland, and with poorly-known Lower Greensand faunas from elsewhere in England. However, other species appear to be endemics.

INTRODUCTION

The Sponge Gravels of Faringdon in Oxfordshire have been worked for at least three hundred years and their rich fauna of Aptian fossils is well known. The earliest recorded collection is that made by Edward Lhuyd (see Edmonds 1973), who was Keeper of the Ashmolean Museum, Oxford between 1690 and 1709. In the early 19th Century, Gideon Mantell collected at Faringdon, but in spite of the fact that many bryozoans collected by him survive in the BM(NH), he made no mention of bryozoan species in either edition (1844, 1854) of his 'The Medals of Creation…'. Sharpe collected extensively at Faringdon and listed 44 bryozoan species in a publication of 1854. Unfortunately he determined his material using d'Orbigny's 'Terrains Crétacés' (1851–54), and his misidentifications led him to believe that the deposit was a remanié of Danian age. Sharpe was the first geologist to describe from Faringdon a new species of bryozoan: *Lopholepis hagenowi* = *Reptoclausa hagenowi* (Sharpe, 1854). Although Meyer (1864) correctly dated the Faringdon deposit as Lower Greensand, the Rev. E. C. Davey largely followed Sharpe's misidentifications of bryozoan species when publishing a catalogue of his collection in 1877. This also listed 44 bryozoan species, though in a later, undated publication (thought from internal evidence to be have been published in the first decade of this century, ?1905) he listed 54 species. Davey sold his collection to the University of Oxford in 1872 (to pay for a law suit) and much of it is still recognizable in the Oxford University Museum. Vine (1891) listed 42 species from Faringdon.

J. W. Gregory described several Faringdon species and mentioned others in the two parts of his catalogue of Cretaceous Bryozoa in the British Museum (1899, 1909*a*). However, no comprehensive systematic work was completed until the publication in 1926 of Canu & Bassler's 'Studies on the cyclostomatous Bryozoa', in which 51 species of bryozoans were distinguished from Faringdon. Canu & Bassler did this joint work entirely by correspondence, sending material backwards and forwards between France and the U.S.A. Their material was collected for them by W. E. Crane; there is no evidence that either author ever visited Faringdon.

One of us (L. J. P.) started to work on the Faringdon bryozoan fauna with the late Henry Dighton Thomas but on the death of Thomas in 1966 this work was suspended. Two short papers (Pitt 1949, 1976) were published on new species from Faringdon before the work of producing a full revision was resumed in 1981 by the two of us.

METHODS AND MATERIAL

In addition to already sorted bryozoan specimens in various institutional collections, much material has been collected and sorted, either from bulk sediment samples or as individual specimens recognizable in the field as bryozoans or potentially bryozoan-encrusted substrates. Ultrasonic cleaning has been employed to remove weakly-adherent matrix, and some specimens have been further developed using a needle. All listed specimens have been examined with binocular microscopes and most of the measurements have been made with an eyepiece graticule. Macrophotographs were prepared from colonies coated lightly in ammonium chloride. Thin sections and acetate peels have been prepared mainly of the cerioporine and cancellate cyclostomes which offer fewer useful external characters. Prior to sectioning most of the specimens were embedded in blocks of resin. A large number of specimens have been studied using an ISI 60A scanning electron microscope (SEM) fitted with a CFAS system. This system enabled study of uncoated specimens, including types, up to about 10 cm in size. The images obtained are formed by back-scattered electrons and have qualities slightly different from conventional secondary electron images (see Taylor 1986*a*). Unless otherwise stated, all photographic illustrations are back-scattered electron micrographs. Magnifications are very approximate.

Institutional abbreviations are as follows: BM(NH), British Museum (Natural History), London; OUM, Oxford University Museum; BGS, British Geological Survey, Keyworth; USNM, United States National Museum (Smithsonian Institution), Washington, USA; MNHN, Muséum National d'Histoire Naturelle, Paris; MHNG, Muséum d'Histoire Naturelle, Geneva; SM, Sedgwick Museum, Cambridge.

For abbreviations of measured morphological characters, see p. 68 (Fig. 2).

GEOLOGICAL SETTING

A small outlier of Lower Greensand (Aptian) occurs in the neighbourhood of Faringdon, 25 km WSW of Oxford (Fig. 1). The Faringdon Lower Greensand (Arkell 1947; Casey 1961 and references therein), resting with unconformity on Kimmeridge Clay or Corallian limestones of Upper Jurassic age, is up to 58 metres thick and is divisible into the following units:

3. Sands with chert and ironstone
2. Sandy clays
1. Sponge Gravel
    b. Red Gravel
    a. Yellow Gravel

Nearly all of the rich fauna comes from the Sponge Gravel, especially the Yellow Gravel. The occurrence of the rare ammonites *Parahoplites nutfieldensis* and *P. maximus* in the Red Gravel (Casey 1961) enables the Faringdon Sponge Gravel to be dated as the lower half of the *nutfieldensis* Zone (*subarcticum* Subzone) of the Upper Aptian.

The Sponge Gravel consists of cross-bedded, bioclast-rich, gravels and sands which are variably ferruginous and differentially cemented. Quartzose, phosphatic and claystone pebbles and cobbles abound, particularly at certain horizons (e.g.

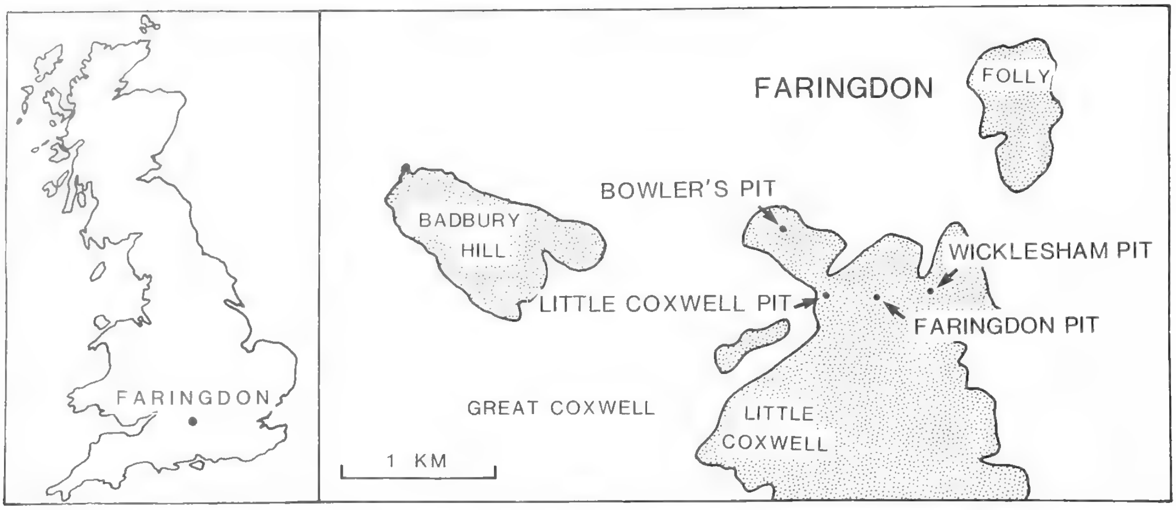


Fig. 1 Locality map of the Faringdon area in Oxfordshire (simplified after Arkell 1947: fig. 28). The outcrop of the Aptian Lower Greensand, which includes the Faringdon Sponge Gravel, is stippled; the remaining unstippled area consists of Jurassic rocks.

near the base of the Red Gravel). The fossils vary in their state of preservation from pristine to fragmented or heavily abraded; some (e.g. belemnites) are clearly derived from the Upper Jurassic. The indigenous fauna is dominated by large calcisponges (notably *Raphidonema* spp.) and other sponges together with bryozoans. Also common are brachiopods (see Middlemiss 1959), oysters, serpulids (see Ware 1975) and echinoids. Aragonitic fossils are generally not preserved, but their past presence is indicated by occasional moulds of gastropods which were overgrown by sponges or bryozoans.

It is thought that the Faringdon Sponge Gravel accumulated in submarine depressions a little way offshore (Arkell 1947). Krantz (1972) made a detailed study of the sedimentology and genesis of the Sponge Gravel, concluding that the deposit represented the transgressive conglomerate of a channel in-filling which incorporated an abundant hardground fauna. The channels were depressions aligned WNW to ESE, formed during an earlier period of marine erosion, and may have represented the 'upstream' end of a tidal, ebb-current dominated bed transport path which operated in a narrow gulf opening to the south and east (Bridges 1982).

Several pits have been worked in the Sponge Gravel (Fig. 1). The best known of these is Little Coxwell Pit (National Grid reference SU 286943) which has yielded the most abundant bryozoan fauna from the Yellow Gravel. Though still accessible at the present day, the workable area of Little Coxwell Pit is now much diminished and lower levels (beneath a cemented horizon) which once yielded the best-preserved material can no longer be reached. The adjacent Faringdon Pit (SU 288943) also exposes the Yellow Gravel, as did the now defunct Bowler's Pit (SU 282947). The large Wicklesham Pit (SU 292944) exposes only the overlying Red Gravel, in which bryozoans are less abundant and generally poorly preserved. There are also small exposures of Yellow Gravel on Badbury Hill (SU 260947).

BRYOZOAN PRESERVATION

Preservation of bryozoans from Faringdon is extremely variable, depending upon both the condition of colonies at the time of burial and subsequent diagenetic factors. Breakage and surficial abrasion occurred in many specimens before burial. Erect branching colonies are invariably preserved as branch fragments commonly less than 1 cm in length. However, rare examples exist of almost intact preservation of arborescent colonies (e.g. Fig. 90). Branch fragments may be extensively abraded, the zooecial frontal walls completely removed in many instances. Even encrusting colonies may be heavily worn and, as in erect colonies, signs of regenerative growth (e.g. Fig. 9B) indicative of pre-mortem fracturing are usually absent; i.e. much of the damage seems to have occurred after colony death (see also p. 65 below). Particularly vulnerable were gynozooecia whose roofs are frequently missing. At the other extreme are encrusting colonies occupying borings or hollows in the substrate in which are preserved very long and delicate peristomes (e.g. Fig. 46). Among erect species, the mixture of fragments showing differing states of preservation suggests more-or-less *in situ* breakdown and abrasion of colonies, the well-preserved fragments having been buried relatively quickly whereas the heavily abraded fragments must have lain for a long time on the sediment surface.

Diagenesis has had an important influence on the preservation of surface details. For example, the best preserved bryozoans show clearly the pseudopores of the frontal walls (e.g. Fig. 16D), and the mural spines which are visible within zooecial apertures (e.g. Fig. 50B). However, slight to profuse growth of crystals of calcite cement obscures these details (e.g. Fig. 26B) in the majority of specimens, particularly those from the Red Gravel. The presence of this cement may be related to dissolution of the aragonitic component of the Faringdon biota. Pressure solution pits (e.g. Fig. 131A, centre left) caused by sand grains juxtaposed to colony surfaces are common and care is needed to prevent these pits being interpreted under the optical microscope as features of bryozoan morphology. Unfortunately many type specimens are poorly-preserved (e.g. Fig. 47) and full characterization of external morphology in these species may be difficult. Calcite overgrowths inside the rims of zooecial apertures (e.g. Fig. 26B) are particularly troublesome when measuring apertural dimensions.

BRYOZOAN PALAEOECOLOGY

Bryozoans are sessile filter-feeders which require a firm substrate for larval settlement and metamorphosis. A wide variety of substrates were utilized by the bryozoans of the Faringdon Sponge Gravel, and this may partly explain the high species diversity. Certain species are characteristic of particular substrates, but others can be found attached to many different types of substrate. Oyster shells, brachiopods (e.g. Fig. 110), sponges (e.g. Fig. 44A) and intraclasts (e.g. Fig. 30) are the most frequently encountered substrates. Large cup-shaped sponges may support colonies of many different species, together with serpulid worms. The absence of an intact substrate in some colonies in which the base is preserved (e.g. Figs 54, 55) may signify attachment during life to a soft-bodied organism, either plant or animal. However, clear bioimmurations revealing the nature of these putative soft substrates have not been found (cf. the Maastrichtian bryozoan fauna described by Voigt, 1973). Echinoid spines are commonly encrusted by bryozoans, particularly *Charixa lhuydi* (see p. 146), which may have been associates of living echinoids. Bones of marine reptiles derived from the Jurassic may also be encrusted by species such as *Idmonea radiolitorum* (Fig. 36).

Wilson (1986) made a detailed study of bryozoans and other organisms encrusting or boring into claystone cobbles from the Red Gravel of Wicklesham Pit. He recognized 23 bryozoan species, most of which were found only within borings and other cavities. These 'coelobites' were apparently able to avoid epifaunal predators and physical abrasion. In contrast, a biota dwelling on cobble surfaces, including the bryozoan *Reptoclausa hagenowi*, is considered by Wilson to have been well-adapted to the rigours of this mobile hard-ground habitat.

Many different bryozoan growth-forms are present in the Faringdon Sponge Gravels. Among the encrusting species, sheet-like (e.g. Fig. 44A), ribbon-like (e.g. Fig. 16A) and runner-like (e.g. Fig. 3A) forms are all represented. Whereas sheet-like colonies have a high commitment to defending the substrate space they occupy, runner-like colonies are fugitives which are well adapted to locating spatial refuges on the substrate, and ribbon-like forms have an intermediate adaptive strategy (see Taylor 1984). Multilamellar growth-forms characterize some sheet-like tubuloporines, and the massive colonies of *Semimulticavea marginata* are also multilayered (Figs 132, 135). Serpulids and other encrusting organisms are frequently found between layers of *S. marginata* colonies; as in some Pliocene cyclostomes with a similar growth-form (Balson & Taylor 1982), these fouling organisms were overgrown and entrapped by their living bryozoan substrates. Colonies of *S. marginata* probably underwent episodic (?seasonal) phases of growth and dormancy (cf. *Multicrescis tuberosa* from the Hauterivian, see Flor & Hillmer 1970). A similar rhythmicity in growth may have characterized colonies of *Reptomulticava brydonei* and *Tholopora* spp. which have subcylindrical branches made up of superimposed subcolonies.

Erect arborescent growth-forms dominate the Faringdon fauna in terms of numbers of species and abundance. Foliaceous growth-forms are notably rare (cf. Walter 1985 on the Neocomian of France and Switzerland), only a solitary fragment of *?Mesenteripora campicheana* being present. All the remaining arborescent bryozoans have subcylindrical, bifurcating branches. These are polarized into a group of species with narrow branches, generally <2 mm in diameter (e.g. Fig. 90), and a less common group of species with robust branches (e.g. Fig. 109). The latter group, comprising *Echinocava raulinii, Heteropora keepingi* and *Ceriopora faringdonensis*, accord with the general observation of McKinney (1986) for thick-branched stenolaemates in possessing maculae which are thought to have been involved in channeling excurrents away from the colony surface.

The narrow-branched arborescent colonies which form the dominant element of the Faringdon fauna fit approximately within the vinculariiform category of growth-forms originally recognized for cheilostome bryozoans. Stach (1936) regarded this growth-form as adapted for life in deep or sheltered waters where wave action is absent and currents are weak. In their classic study of bryozoan growth-forms in the Recent sediments off the Rhône Delta, Lagaaij & Gautier (1965) found that vinculariiform bryozoans reached their highest percentages in deep-water (>120 m) calcareous sands, although minor percentages of this growth-form occurred across most of the area of study. Wass, Conolly & Macintyre (1970), working in southern Australia, noted that vinculariiform colonies commonly occurred at depths greater than 100 fathoms (*c.*180 m). However, it is unclear to what extent these environmental findings for Recent cheilostome-dominated faunas can be applied to the cyclostome assemblage of the Faringdon Sponge Gravel.

A quantitative study of fragments of 'vinculariiform' cyclostomes in samples of Yellow Gravel from Little Coxwell Pit has been undertaken by A. Butterworth, whose unpublished results are summarized here. In a sample from the A. G. Davis Collection, 40% of fragments were unidentifiable (usually because they were excessively worn), and of the 11 species distinguished in the identifiable portion, *Meliceritites dendroidea* and *Ceata granulata* were the most common, accounting for 14% and 13% respectively by weight of the sample. As might have been expected, the mean length of fragments of each species correlated strongly with the average branch thickness for that species; i.e. species with thin branches were broken into shorter fragments than species with thick branches. Counts were made of the number of fragments preserving growth tips and the number preserving branch bifurcations (Y-shaped fragments). Topological considerations dictate that the number of bifurcations in an arborescent colony should equal one less than the number of growth tips (see Cheetham, Hayek & Thomsen 1981: 78). As Faringdon bryozoan colonies were comparatively large when intact, in the absence of sorting the number of bifurcating fragments present in any given sample of branch fragments resulting from the mechanical breakdown of colonies should approximate to the number of growth tips present. This was found not to be so in the samples analysed. In the A. G. Davis sample, 249 bifurcations as against 37 growth tips were counted; i.e. bifurcations were 6·7 times as common as growth tips. A larger sample collected by one of us (P. D. T.) in 1985 yielded 721 bifurcations and only 210 growth tips; bifurcations were 3·4 times as common as growth tips. This under-representation of growth tips can be explained in two ways: by net transportation of growth tips away from the site of deposition (e.g. by branch tips breaking off in-situ colonies mechanically or as a result of the activity of predators), or by loss of growth tips during mechanical abrasion of colony fragments prior to their burial. The second interpretation is favoured because the more delicate species (e.g. *Entalophoroecia quadripartita, Siphodictyum gracile*) were found to

Table 1 List of bryozoan species from the Faringdon Sponge Gravel described in this paper, with a comparative list of names used by Canu & Bassler (1926) for these species.

This paper	Canu & Bassler, 1926
'Stomatopora' melvillei sp. nov.	—
Stomatoporina alternata sp. nov.	—
Voigtopora calypso (d'Orbigny)	*Stomatopora calypso* (d'Orbigny)
Stomatoporid sp. 1	—
Stomatoporid sp. 2	—
Proboscinopora marginata (d'Orbigny)	—
Oncousoecia coarctata (Canu & Bassler)	*Proboscina coarctata* sp. nov.
Oncousoecia depressa (d'Orbigny, *sensu* Canu & Bassler)	*Proboscina depressa* (d'Orbigny)
Oncousoecia parvula (Canu & Bassler)	*Berenicea parvula* sp. nov. *Microecia cornucopia* (d'Orbigny) *Proboscina virgula* (d'Orbigny)
Filisparsa gasteri sp. nov.	—
Reptoclausa hagenowi (Sharpe)	*Reptoclausa hagenowi* (Sharpe)
Idmonea denticulata (Canu & Bassler)	*Reptoclausa denticulata* sp. nov.
Idmonea radiolitorum d'Orbigny	*Proboscina radiolitorum* (d'Orbigny) *Proboscina zic-zac* d'Orbigny
Collapora hillmeri sp. nov.	—
Plagioecia orbifera (Canu & Bassler)	*Diaperoecia orbifera* sp. nov. *Berenicea pulchella* de Loriol (*partim*) *Berenicea (Reptomultisparsa) tenella* de Loriol
Plagioecia spissa (Gregory)	*Cellulipora spissa* (Gregory)
Hyporosopora constricta sp. nov.	—
Hyporosopora larwoodi sp. nov.	—
Hyporosopora mantelli sp. nov.	*Trigonoecia haimei* (de Loriol)
Mesonopora fecunda (Vine)	—
Cardioecia neocomiensis (d'Orbigny)	*Cardioecia faringdonensis* sp. nov. *Cardioecia pauper* sp. nov. *Notoplagioecia faringdonensis* sp. nov.
Ceata granulata (Canu & Bassler)	*Cea granulata* sp. nov.
?Mesenteripora campicheana (d'Orbigny)	—
Entalophoroecia quadripartita (Canu & Bassler)	*Clinopora quadripartita* sp. nov.
Unitubigera sp.	—
Meliceritites gracilis (Goldfuss)	—
Meliceritites dendroidea (Keeping)	*Lobosoecia semiclausa* (Michelin) *Meliceritites semiclausa* Gregory
Meliceritites cunningtoni (Gregory)	*Meliceritites cunningtoni* (Gregory)
Meliceritites transversa Canu & Bassler	*Meliceritites transversa* sp. nov.
'Berenicea' filifera Canu & Bassler	*Berenicea filifera* sp. nov.
'Berenicea' faringdonensis Canu & Bassler	*Berenicea faringdonensis* sp. nov.
'Berenicea' grandipora Canu & Bassler	*Berenicea grandipora* sp. nov.
'Berenicea' cf. *sowerbyi* (Lonsdale)	—
Siphodictyum gracile Lonsdale	*Siphodictyum gracile* Lonsdale *Siphodictyum irregulare* sp. nov.
Laterocavea dutempleana d'Orbigny	*Laterocavea dutempleana* d'Orbigny
Laterocavea? intermedia Canu & Bassler	*Laterocavea intermedia* sp. nov. *Clausa cranei* sp. nov.
Heteropora clavata, *sensu* Gregory	—
Heteropora keepingi Gregory	*Ceriopora dimorphocella* sp. nov. [?] *Heteropora nummularia* sp. nov.
Ceriopora farringdonensis Gregory	—
Tetrocycloecia multiporosa Canu & Bassler	*Tretocycloecia (?) multiporosa* sp. nov. *Tretocycloecia densa* sp. nov.
Clausa zonifera Canu & Bassler	*Clausa zonifera* sp. nov.
Semimulticavea marginata (Canu & Bassler)	*Multigalea marginata* sp. nov. *Multigalea canui* (Gregory) *Radiopora tuberculata* (d'Orbigny)
Seminodicrescis variolata (Gregory)	*Multicrescis mammilosa* sp. nov. *Seminodicrescis nodosa* d'Orbigny
Reptomulticava brydonei (Gregory)	*Reptomulticava fungiformis* Gregory
Tholopora dightoni sp. nov.	*Tholopora virgulosa* Gregory
Tholopora hastingsae sp. nov.	—
Tholopora thomasi Pitt	—
Echinocava raulinii (Michelin)	*Plethopora aptensis* sp. nov.
Paracrescis boardmani sp. nov.	—
Charixa lhuydi (Pitt)	—

have particularly low ratios of growth tips to bifurcations. Pre-burial abrasion of branch fragments was an important aspect of bryozoan taphonomy in the Faringdon Sponge Gravel.

Factors contributing to the richness of the Faringdon bryozoan fauna may have included:

1. High availability of hard substrates for attachment; 'primary' substrates may have been supplied by the erosion of fossils and concretions from the underlying Jurassic sediments, and 'secondary' substrates by the variety of organisms that developed on these primary substrates. The abundance and variety of substrates at Faringdon probably added to bryozoan richness, as Eggleston (1972) found for communities of Recent bryozoans living off the Isle of Man.
2. Episodic sedimentation allowing sufficient time for the colonization of the sea-bed by epibenthos before swamping and burial by migrating sandwaves.
3. Paucity of fine-grained sediment deposition.
4. Provision of nutrient-laden currents (cf. the present-day Otago Shelf of New Zealand where bryozoans attain maximum densities in areas in the path of the Southland Current according to Probert, Wilson & Batham 1979).

FAUNAL COMPOSITION AND COMPARISONS

The Faringdon fauna is the most diverse bryozoan fauna of early Cretaceous age currently recognized from anywhere in the world. A total of 50 calcareous bryozoan species are recognized (Table 1), all cyclostomes with the exception of a single cheilostome. To these must be added a boring ctenostome bryozoan described by Voigt & Soule (1973) as *Terebripora* (?) *bassleri* and questionably re-assigned to *Ropalonaria* by Pohowsky (1978). This figure of diversity compares with the 50 species listed by Canu & Bassler (1926: 2–3). However, some additional species are here recognized while several of those listed by Canu & Bassler are placed in synonymy. Canu & Bassler's neuroporid species (*Neuropora micropora, N. tenuinervosa, Neuroporella hemispherica*) are now thought to be sclerosponges rather than bryozoans (Kaźmierczak & Hillmer 1974), as is a fourth Faringdon species (not listed by Canu & Bassler) described by Gregory (1909*b*, see also 1909*a*) as *Reptomulticava fungiformis*.

Ryland (1970: 134) regarded the Lower Cretaceous as the zenith of the cyclostome bryozoans. Indeed, both the Faringdon cyclostome fauna and the diverse Valanginian fauna of Sainte-Croix in Switzerland (from which Walter (1972) recorded 37 species here regarded as cyclostomes) are appreciably richer in species than are the most diverse cyclostome faunas known from the Jurassic (see Walter 1970) or the pre-Jurassic. Although highly diverse bryozoan faunas continue into the Upper Cretaceous these contain an increasing proportion of cheilostomes which attain dominance over cyclostomes by about the end of the Santonian.

In terms of higher taxa, the Faringdon cyclostome fauna is dominated by tubuloporines (including melicerititids) of which there are 33 species (67%). The other cyclostome suborders are represented as follows: cerioporines—11 species (23%); cancellates—4 species (8%); rectangulates—1 possible species (2%). It should be noted, however, that the status of these suborders is currently that of evolutionary grades and not clades. Analysis of phylogenetic relationships in cyclostomes has yet to be attempted even at the most basic level.

Other Aptian bryozoan faunas in Britain are very poorly known. Although Casey (1961) gives a long list of species recorded from the British Aptian, many of these are species described by Canu & Bassler (1926) and known only from Faringdon. The work of Keeping (1883) on bryozoans from the Aptian of Upware (Cambridgeshire) and Brickhill (Bedfordshire) is greatly in need of revision. Both localities are now no longer accessible, but the material described by Keeping survives in the collections of the Sedgwick Museum, Cambridge. Keeping records 18 bryozoan species from Upware and 8 from Brickhill. At least two of the Upware species (*Meliceritites dendroidea* (Keeping) and *Echinocava raulinii* (Michelin)) occur also at Faringdon. Also in need of revision are the four putative bryozoan species described by Lonsdale (1849), apparently from the Atherfield Clay (Lower Aptian) of the Isle of Wight. These include *Siphodictyum gracile* Lonsdale which is a common species in the Faringdon Sponge Gravel. The BM(NH) collections contain a significant number of bryozoan specimens, many poorly-preserved, from Aptian Lower Greensand localities in Kent and Surrey. These too are in need of study.

Outside Britain Aptian bryozoans are mostly known from SE France and the Jura where Walter and colleagues have made several faunal studies (Delamette & Walter 1984; Masse & Walter 1974; Walter 1977; Walter & Busnardo 1971; Walter & Clavel 1979; Walter *et al.* 1975). It is difficult to assess how many species are shared between Faringdon and these French and Swiss localities. However, the following distinctive species occur in common: *Siphodictyum gracile* Lonsdale, *Laterocavea dutempleana* d'Orbigny, *Echinocava raulinii* (Michelin) and *Cardioecia neocomiensis* (d'Orbigny). All of these appear to be long-ranging species; *S. gracile* is recorded from the Barremian and Aptian (Walter *et al.* 1975), *L. dutempleana* from the Aptian and Albian (Voigt 1981), *E. raulinii* from the Hauterivian to Albian (Walter *et al.* 1975), and *C. neocomiensis* from the Hauterivian to Aptian (Hillmer 1971).

A considerable number of species found at Faringdon have not been recorded elsewhere. Whether or not these are truly endemic will only become clear after further studies of Lower Cretaceous bryozoan faunas. Among the more distinctive species apparently restricted to the Faringdon Sponge Gravels are the following: *Idmonea denticulata, Reptoclausa hagenowi, Meliceritites cunningtoni, Paracrescis boardmani*, and the three species of *Tholopora*.

SYSTEMATIC PALAEONTOLOGY

All known species of calcareous bryozoans present in the Faringdon Sponge Gravel are described. For description of the boring ctenostome *Terebripora* (?) *bassleri* Voigt & Soule, see Voigt & Soule (1973: 24) and Pohowsky (1978: 57).

Although this faunal study is not intended as a monographic revision of any particular taxa of cyclostomes, it has been necessary to make remarks concerning the status of many genera and the concepts of the genera as here employed. Problems encountered in defining genera emphasize the need for thorough revisions of generic type species, as done by Nye

(1976) for some of the cerioporine genera. Unfortunately many of these type species were founded by d'Orbigny (1851–54), who used large syntypic suites of specimens from more than one locality when describing his new species. Not only is it usually difficult or impossible to match any one syntype to d'Orbigny's stylized published figures, but each syntypic suite may comprise more than one species. A full revision of the d'Orbigny Collection (housed in the MNHN, Paris) is of paramount importance to the future progress of systematic studies of Cretaceous cyclostomes.

The generic ranges quoted below are highly tentative but are believed to represent an improvement in precision and accuracy on previously published data (Bassler 1953).

Abbreviations of measured morphological characters are shown in Fig. 2 and its caption. Additional abbreviations used in the text but not shown on this figure are: **BW**, branch width; **KAM**, kenozooecial apertural measurement; **LOPM**, longitudinal ooeciopore measurement; **LOSM**, longitudinal ooeciostome measurement; **TOPM**, transverse ooeciopore measurement; **TOSM**, transverse ooeciostome measurement.

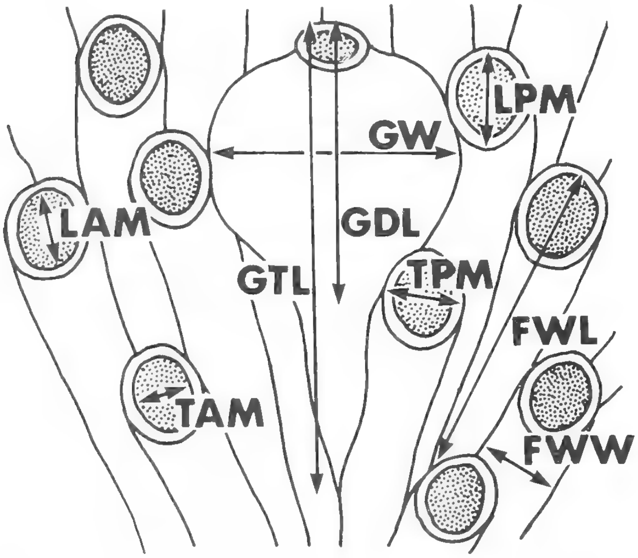


Fig. 2 Measured morphological characters in cyclostome bryozoans from the Faringdon Sponge Gravel. Abbreviations: **FWL**, frontal wall length (of autozooecia); **FWW**, frontal wall width; **GDL**, gynozooecium dilated length; **GTL**, gynozooecium total length; **GW**, gynozooecium width; **LAM**, longitudinal apertural measurement (of autozooecia); **LPM**, longitudinal peristome measurement; **TAM**, transverse apertural measurement; **TPM**, transverse peristome measurement.

It should be noted that measurements of zooecial and zoarial dimensions have generally been made from a limited number of specimens and may not encompass the entire range of values present in the species. Pseudopore densities have been calculated by placing a square of known area over SEM prints at a standard magnification of × 320, counting the number of pseudopores present and calculating how many would be present in an area of one mm^2.

To assist species identification, the key in the Appendix (p. 149) should be consulted.

Unless otherwise stated, all listed material is from the Faringdon Sponge Gravel of the Faringdon area. Exact locality and collection details are given when known. In cases where more than one specimen has been registered under a single number, this is indicated by a number or the word 'sample' in parenthesis after the specimen registration number.

Order **CYCLOSTOMATA** Busk, 1852
Suborder **TUBULIPORINA** Milne Edwards, 1838
Family **STOMATOPORIDAE** Pergens & Meunier, 1886

Genus ***STOMATOPORA*** Bronn, 1825

TYPE SPECIES. *Alecto dichotoma* Lamouroux, 1821, by monotypy; Bathonian, France.

REMARKS. *Stomatopora* is here used for encrusting uniserial or nearly uniserial tubuliporines lacking basal gynozooids. Different authors have applied the name in different ways; for example, Harmelin (1974*a*) included Recent species with peristomial gynozooids, Walter (1970) Jurassic species with erect branches, and Illies (1973) species exhibiting a variety of budding patterns. These interpretive problems arise in part because the type material of the type species was destroyed during the battle for Caen in 1944. Although Walter (1970) proposed a neotype for *Stomatopora dichotoma* (see Illies 1976), it is by no means clear whether this is conspecific with Lamouroux' original material. Also, the lack of peristomial gynozooids in fossil material may be a result of preservational factors rather than primary absence. Until the precise identity of the genus has been clarified, *Stomatopora* can be only loosely applied and it seems appropriate to write the name in quotations.

Early branches of the neotype of *S. dichotoma* are uniserial but later branches are narrowly multiserial with the proximal parts of later budded zooecia occurring side-by-side with the distal parts of earlier zooecia. The distinction between *Stomatopora* and the more obviously multiserial new genus *Proboscinopora* (see p. 74) is somewhat gradational, although in *Proboscinopora* zooecia budded at the same level often have their apertures side-by-side.

RANGE. Triassic (Carnian) to Recent.

'Stomatopora' melvillei sp. nov. Figs 3–6

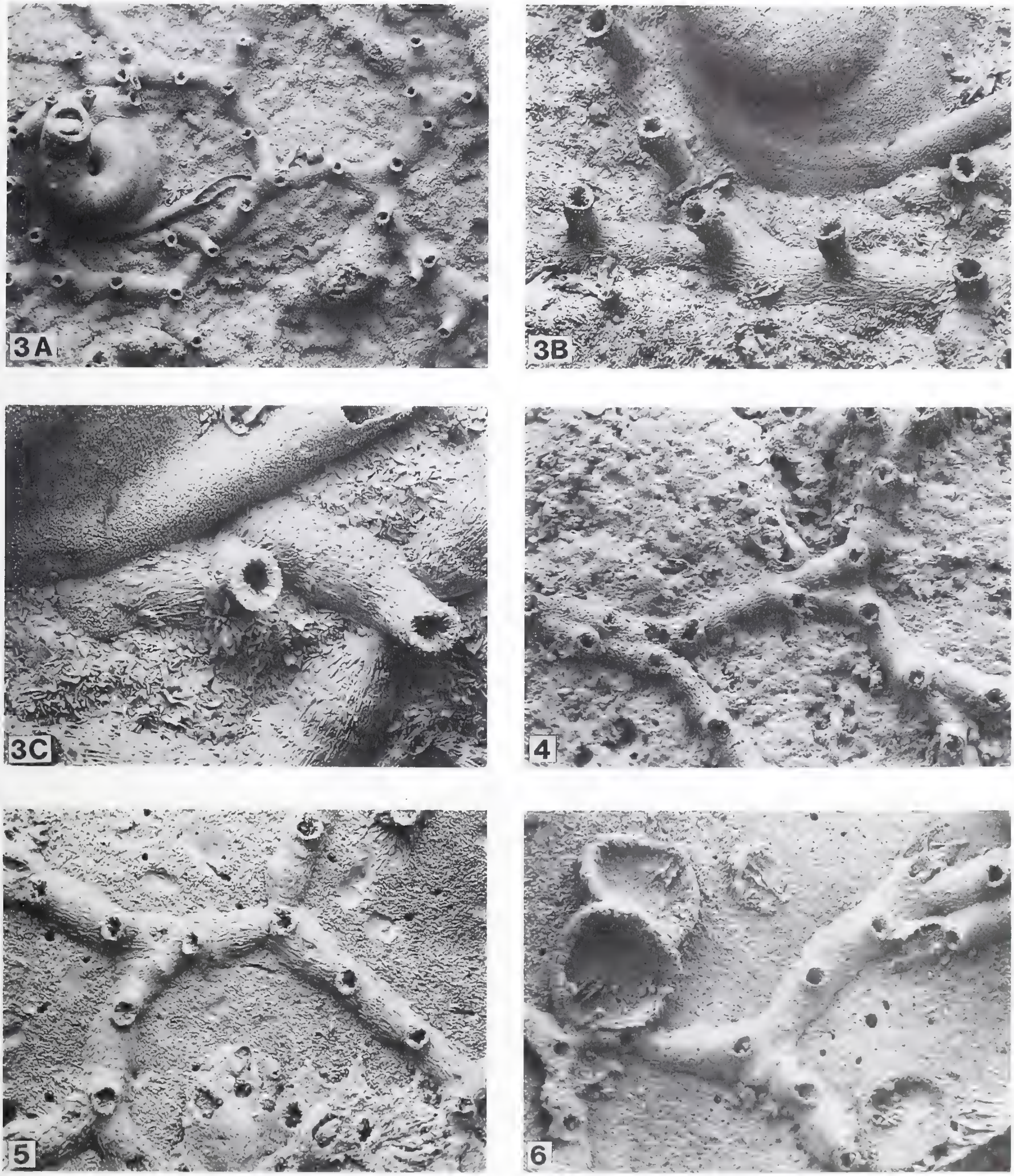
1899 *Proboscina crassa* (Roemer) var. *divaricata* (d'Orbigny); Gregory: 35 (*partim*); pl. 2, fig. 8.

HOLOTYPE. BM(NH) D53699, Faringdon Sponge Gravel, Little Coxwell Pit, A. G. Davis Colln.

PARATYPES. BM(NH) 60538, Cunnington Colln (figured by Gregory 1899: pl. 2, fig. 8, as *Proboscina crassa* var. *divaricata*); D6322, D6326, A. N. Davis Colln; D7979, D7982, Treacher Colln; D55111, D55358–9, D55361–2, Little Coxwell Pit, Gaster Colln; D55357, D55360, Bowler's Pit, Gaster Colln.

NAME. For Richard V. Melville, in recognition of his research on the Faringdon Sponge Gravel.

DESCRIPTION. Zoarium encrusting, with uniserial branches in early growth stages but in later stages branches are often biserial, particularly immediately after their division. The first internode consists of the ancestrula and one other zooid. Thereafter, branches bifurcate at variable intervals, with between 1 and 9 zooecia per internode. The first bifurcation is at a high angle (130°–170°), but later bifurcations occur at decreasing angles; e.g. in BM(NH) D6326 the first bifurcation angle is 170°, the second averages 125°, the third 116°, the



Figs 3–6 *'Stomatopora' melvillei* sp. nov. Fig. 3, BM(NH) D53699, **holotype**; 3A, early zooecia sharing the same substrate as some serpulid worms, × 14; 3B, zooecia with well-preserved peristomes, × 27; 3C, ancestrula and first budded zooecium, × 60. Fig. 4, BM(NH) D6322, branch bifurcations with adherent sibling zooecia, × 15. Fig. 5, BM(NH) D6326, × 23. Fig. 6, BM(NH) D7979, broad zooecia budded during late astogeny, × 20.

fourth 85°, and the fifth 105°. Angles in late astogeny are occasionally so low that the two sibling zooecia are adherent for much of their lengths (Fig. 4).

Zooecia are moderately large, slender, almost parallel-sided, with smooth, convex frontal walls bearing large pseudopores (approximately 900 per mm^2). Apertures are circular and moderately large. Peristomes may be well-raised, up to 0·25 mm when preserved in recesses on the substrate.

The ancestrula is present in BM(NH) D55111 in which the protoecium has a transverse diameter of 0·29 mm and the ancestrula a total length of 0·56 mm. A partly overgrown ancestrula occurs in BM(NH) D53699 (Fig. 3C). The primary

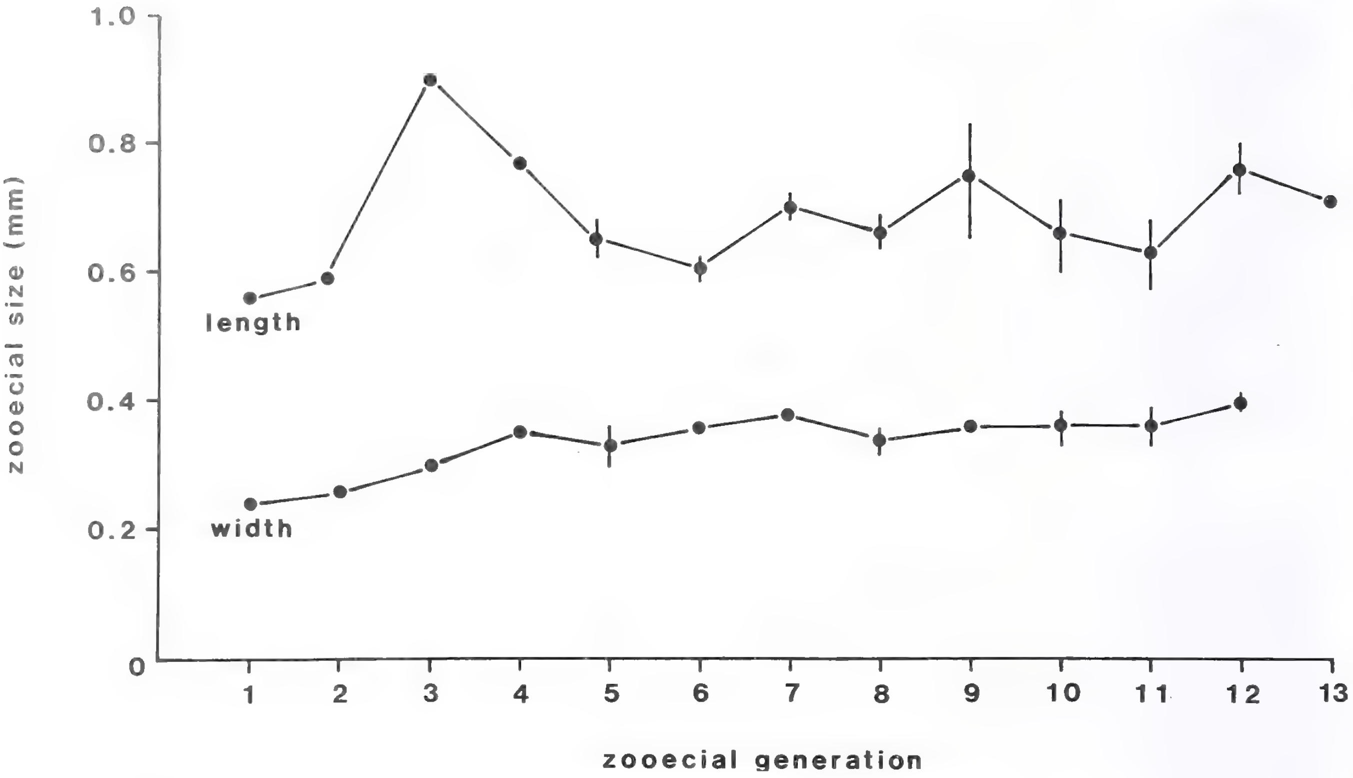


Fig. 7 Astogenetic gradients of zooecial length and width in a colony of *'Stomatopora' melvillei* sp. nov., BM(NH) D55111.

zone of astogenetic change for zooecial length is poorly differentiated and possibly brief, with relatively little difference in size between zooecia of different generations (Fig. 7). Zooecial width increases at a low rate for 10 or more zooecial generations.

MEASUREMENTS. TAM, 0·12–0·16 mm; TPM, 0·18–0·26 mm; FWL, 0·60–0·90 mm; FWW, 0·24–0·45 mm.

REMARKS. This species resembles the *S. granulata* (Milne Edwards, 1838) of Walter (1972: 293–294) but has shorter zooecia. It differs from *S. incrassata* (d'Orbigny, 1850) in the smaller zooecial dimensions.

'S.' melvillei is a common species at Faringdon and can be found encrusting a wide variety of substrates. It is most likely to be confused with *Voigtopora calypso* (below), which has zooecia of similar size. However, the parallel-sided zooecia of *'S.' melvillei* contrast with the slightly barrel-shaped zooecia of *V. calypso*, branches of *V. calypso* are never biserial, and lateral branching is known only in *V. calypso*.

Genus *VOIGTOPORA* Bassler, 1952

TYPE SPECIES. *Alecto calypso* d'Orbigny, 1850, by original designation; Senonian of Saintes, Charente-Maritime, France.

REMARKS. Illies (1976) has redescribed the type species of *Voigtopora*. This genus differs from typical *Stomatopora* principally in the occurrence of lateral branching. *Voigtopora* also has zooecia which extend proximally as long, narrow tubes flanking the proximal zooecium.

RANGE. Aptian (?Hauterivian) to Campanian.

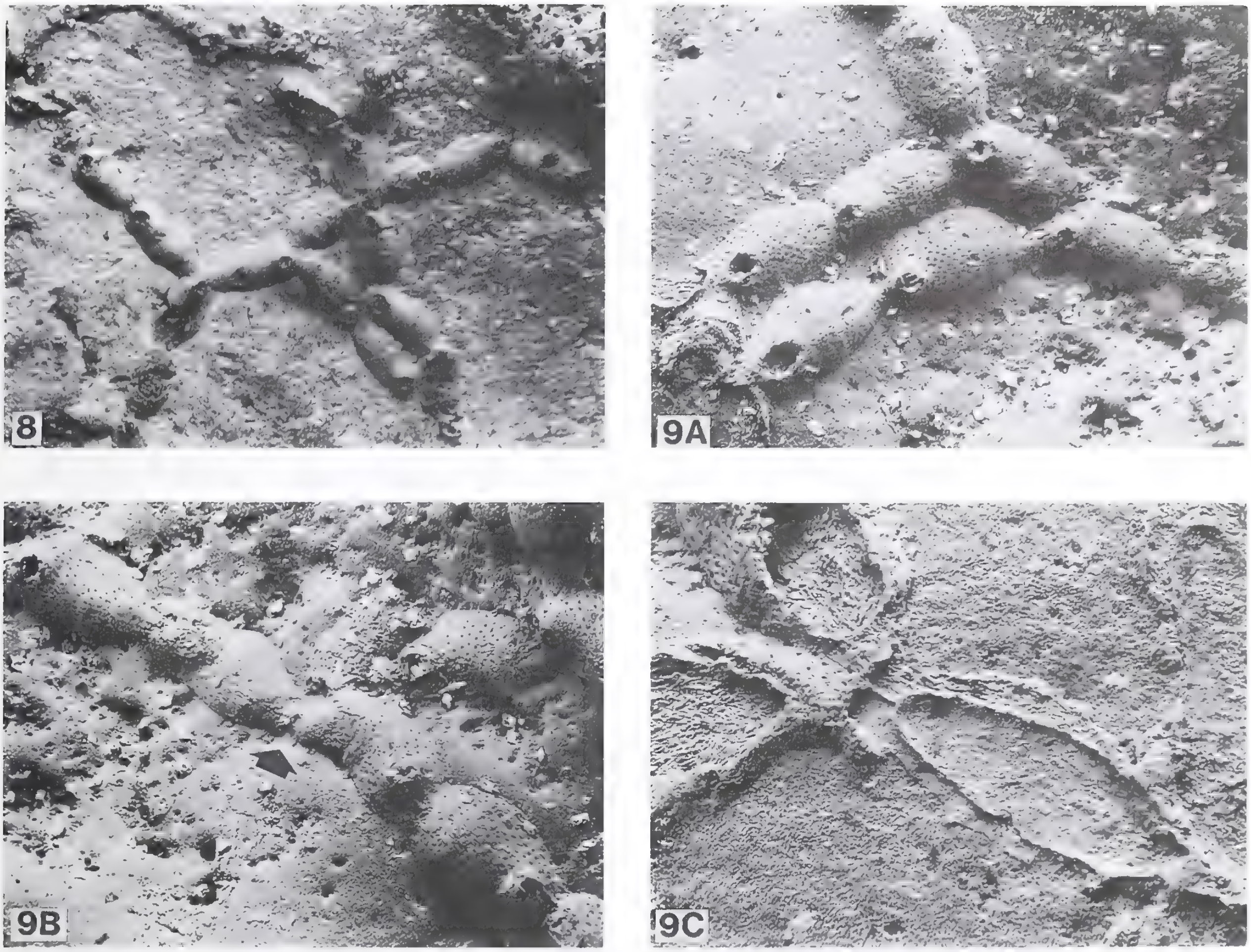
Voigtopora calypso (d'Orbigny, 1850) Figs 8–12

1850 *Alecto calypso* d'Orbigny: 265.
1851 *Alecto calypso* d'Orbigny; d'Orbigny: 844; pl. 630, figs 5–8.
1853 *Stomatopora calypso* (d'Orbigny) d'Orbigny: 841.
1926 *Stomatopora calypso* (d'Orbigny); Canu & Bassler: 5; pl. 26, fig. 11.
1974 *Voigtopora? calypso* (d'Orbigny) Illies: 133; fig. 2c.
1976 *Voigtopora calypso* (d'Orbigny); Illies: 108; figs 4–8.
1986 *Stomatopora calypso, sensu* Canu & Bassler; Wilson: 693.

MATERIAL. BM(NH) D7978, Treacher Colln; 60537a-b, Cunnington Colln; D55353, Little Coxwell Pit, A. G. Davis Colln; D55354, Little Coxwell Pit, Thomas Colln; D55355–6, Little Coxwell Pit, Gaster Colln; D52149, D57394, Little Coxwell Pit; D57418, Wicklesham Pit, Pitt Colln; D57736, Little Coxwell Pit, Voigt Colln.

DESCRIPTION. Colony encrusting, uniserial, branches generally dividing dichotomously at an angle of about 90°, with two to three zooecia occupying each internode. Rare lateral ramifications occur, daughter branches making an angle of about 90° to their parent branch. The ancestrula (observed only in D57736) buds a distal zooecium, and apparently two adventitious zooecia, one arising proximally (which is worn) and one laterally from the protoecium (Fig. 10A). The ancestrula has a protoecium 0·21 mm in diameter, and has a total length of 0·40 mm. A 'bipolar zooid pair' (*sensu* Taylor 1986*c*) consisting of two zooecia joined at their proximal ends (Fig. 9B) in one specimen indicates regenerative branch growth following damage.

Zooecia are moderately large, rather barrel-shaped in



Figs 8–9 *Voigtopora calypso* (d'Orbigny). Fig. 8, BM(NH) 60537, overgrowing branches, × 15. Fig. 9, BM(NH) D7978; 9A, barrel-shaped zooecia, × 28; 9B, bipolar pair of zooecia (junction arrowed), × 25; 9C, abraded zooecium preceeding a branch bifurcation and showing septal traces of the proximal parts of the daughter zooecia, × 50.

outline, sometimes with transverse wrinkles on the frontal wall. Most zooecia have a proximal portion, normally visible only in abraded specimens, of two narrow 'prongs' flanking the next proximal zooecium in linear series (Fig. 9C). However, each of the two daughter zooecia following branch dichotomy has only one 'prong' lateral to the proximal zooecium. Zooecial apertures are small and circular, and peristomes are usually only slightly raised, although a peristome 0·45 mm in length has been observed in a recess in the substrate. When visible pseudopores are large and circular (approximately 600 per mm^2).

Measurements. TAM, mean 0·06 mm; TPM, mean 0·14 mm; FWL, mean 0·80 mm; FWW, mean 0·46 mm.

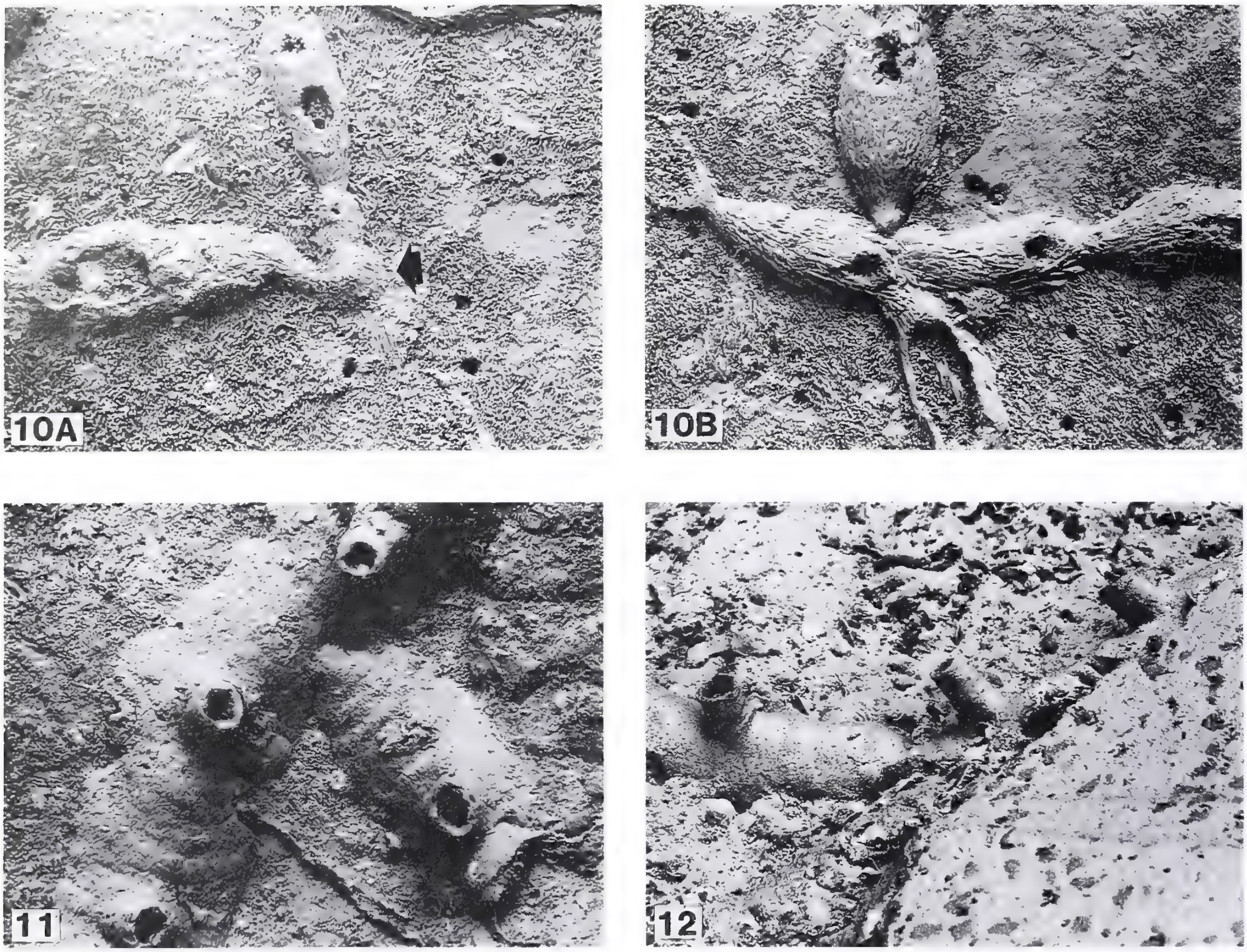
Remarks. This species is very common in the Faringdon Sponge Gravel, and can be found encrusting phosphatic pebbles and other substrates. Colonies are characteristically fragmentary and early growth stages are usually absent.

Lateral ramifications (Figs 10B, 11), the principal diagnostic character of *Voigtopora*, occur very infrequently in Faringdon populations of *V. calypso*. Early growth stages are unknown in type and other material of *V. calypso* from the Santonian of France. In the single known Faringdon colony to preserve early growth stages, a lateral and apparently a proximal bud (which is worn) emerge from the protoecium. Conspecific colonies from the Cenomanian of the Le Mans area have one of two growth patterns in early astogeny: in some colonies the ancestrula produced a proximal bud from the protoecium (cf. Illies 1974 in *Stomatopora multigemmans*); in other colonies such a bud is absent and a proximally growing branch arose as a strongly reflexed lateral branch from one of the early post-ancestrular zooecia. A population from the Cenomanian Del Rio Clay of Texas consists entirely of colonies with the second pattern.

Genus *STOMATOPORINA* Balavoine, 1958

Type species. *Alecto incurvata* Hincks, 1860, by original designation; Recent (see Hayward & Ryland 1985).

Remarks. *Stomatoporina* is characterized by colonies of uniserial, spiralling branches formed by zooecial budding along one margin of the branch only, but sometimes developing straight, biserial branches in later astogeny with zooecia budding from either side of the median line of the branch (see Illies 1975). Apart from the type species, one other species has been referred to the genus, *Stomatoporina spirata* (Walford) from the Middle Jurassic of Shipton Gorge, Dorset (Illies 1975).



Figs 10–12 *Voigtopora calypso* (d'Orbigny). Fig. 10, BM(NH) D57736; 10A, ancestrula (protoecium arrowed) giving rise to a distal zooecium and a left lateral zooecium which emerges from the protoecium, × 39; 10B, bifurcation and lateral ramification, × 32. Fig. 11, BM(NH) D57394, lateral ramification, × 40. Fig. 12, BM(NH) D57418, oblique view of zooecia with long peristomes, × 32.

RANGE. Bajocian to Recent.

Stomatoporina alternata sp. nov. Figs 13–15

HOLOTYPE. BM(NH) D55352, Little Coxwell Pit; Gaster Colln.

PARATYPES. BM(NH) D55348, D53225, Little Coxwell Pit, Taylor Colln; B1935 (2 colonies on *Neuropora* sp.), Little Coxwell Pit, Lee Colln.

NAME. 'By turns'.

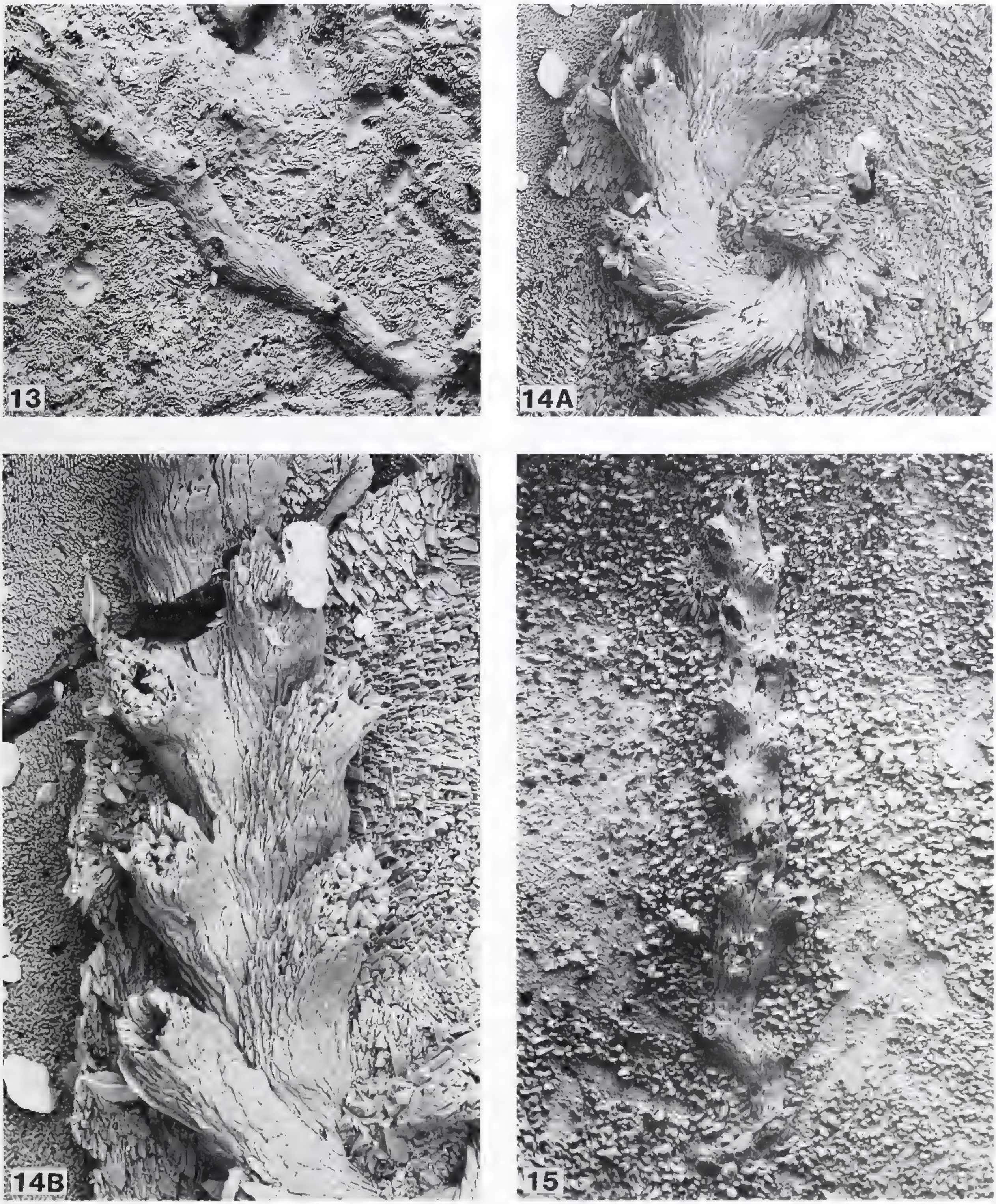
DESCRIPTION. Zoarium encrusting, initially uniserial (Fig. 14A) with zooecial apertures opening on one side; later biserial, with zooecia budding alternately to the left and right sides of the narrow branches (Fig. 13), which zigzag gently. Branches are 0·12 to 0·25 mm wide and bifurcate dichotomously at 60°–90°. Both daughter branches are biserial. Internodes are generally long, e.g. BM(NH) D55348 preserves the colony origin and about 16 generations of zooecia in a branch 3 mm long which does not bifurcate.

Zooecia are small, short in the early stages of the zoarium but longer in later stages, slender, proximally tapering, with circular apertures. Peristomes are offset from the midline of the branches and slightly raised. Pseudopores are not clearly visible in the poorly-preserved material available. The ancestrula, known from two abraded examples, is about 0·27 mm long and has an apertural diameter of 0·07 mm and a protoecium 0·12 mm in transverse width. Gynozooecia have not been observed.

MEASUREMENTS. TAM, 0·04–0·06 mm; TPM, 0·07–0·09 mm; FWL, 0·38–0·60 mm; FWW (proximal), 0·12–0·15 mm.

REMARKS. This new species appears to be the only described Cretaceous stomatoporid with a biserial budding pattern of regularly alternating, zigzag zooecia. There is a close resemblance with *Stomatoporina spirata* (Walford) from the Bajocian, redescribed by Illies (1975), which can show both uniserial and biserial growth, the uniserial branches taking the form of a tight spiral of zooecia. However, *S. alternata* differs in having longer zooecia, and in dichotomizing to give two biserial daughter branches; biserial branches in *S. spirata* divide to give one biserial daughter and one lateral daughter branch which is uniserial.

Within species variation in zooecial length has a considerable effect on the morphology of branches. Colony BM(NH) D53225 has relatively short zooecia and the branches consequently appear wider and have apertures more closely-spaced than is usual.



Figs 13–15 *Stomatoporina alternata* sp. nov. Fig. 13, BM(NH) D55352, **holotype**, × 41. Fig. 14, BM(NH) D53325; 14A, spiral arrangement of coarsely-preserved early zooecia, × 72; 14B, zooecia opening alternately to left and right, × 119. Fig. 15, BM(NH) D55348, small weathered colony, × 39.

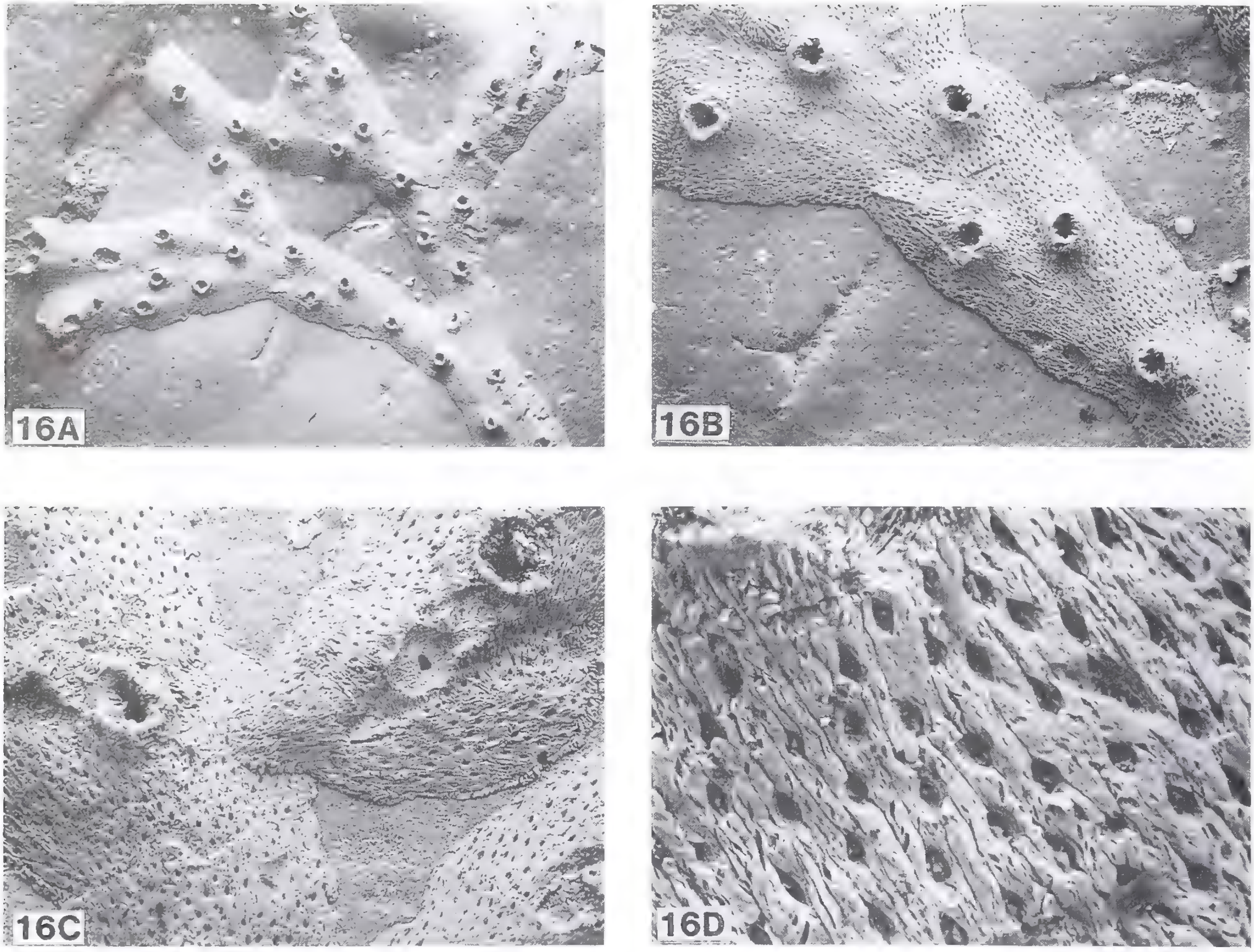


Fig. 16 *Proboscinopora marginata* (d'Orbigny), BM(NH) D7982; 16A, bifurcating and anastomosing branches, × 17; 16B, medial autozooecia flanked by kenozooecia whose outlines are not visible, × 32; 16C, origin of a lateral ramification, × 64; 16D, pseudopores, × 290; see also Fig. 17.

Genus *PROBOSCINOPORA* nov.

TYPE SPECIES. *Proboscina divisi* Vine, 1893; Middle Jurassic, Cornbrash (probably basal Callovian), Thrapston, Northamptonshire.

DIAGNOSIS. Colony encrusting with regularly oligoserial branches which may bifurcate and occasionally produce lateral ramifications; basal gynozooecia lacking.

NAME. Like *Proboscina*.

REMARKS. Among Mesozoic and Cenozoic cyclostomes generally referred to the genus *Proboscina* Audouin, 1826 are several species in which gynozooecia have not been found in spite of the availability of large populations for study. Although recognizing the need for a new genus to accommodate such multiserial stomatoporids, Canu & Bassler (1920: 659) followed the tradition of using the name *Proboscina* while acknowledging that the type species of *Proboscina*, the Recent *P. boryi* Audouin, possessed a gynozooecium. In order to 'conserve' the name *Proboscina* for species without gynozooecia, they erected a new genus *Peristomoecia* (1920: 692) for *Proboscina*-like species possessing gynozooecia. *Peristomoecia* comprised, as well as its type species *Stomatopora divergens* Waters, 1904, two other species, one of which was *Proboscina boryi*. By this action they made *Peristomoecia* a subjective junior synonym of *Proboscina*, and did not solve the problem of the need for a genus to accommodate probosciniiform species lacking gynozooecia. Therefore, the new genus *Proboscinopora* is here created for species with colonies resembling those of *Proboscina* but lacking basal gynozooecia. These stomatoporids are characterized by their ribbon-like, narrowly multiserial (oligoserial) branches which maintain a relatively constant width and bifurcate at intervals. Branches are usually of low profile and smooth-surfaced.

The species composition of *Proboscinopora* has yet to be fully established; many species which possibly belong to the genus are too poorly described or known from too few specimens for the absence of basal gynozooecia to be inferred with confidence.

RANGE. Uncertain; species are known to occur in the British Bathonian, and at least one species, *Proboscinopora toucasiana* (d'Orbigny), is found in the Upper Cretaceous (Coniacian–Santonian, ?Campanian).

Proboscinopora marginata (d'Orbigny, 1853)

Figs 16–17

1853 *Proboscina marginata* d'Orbigny: 849; pl. 631, figs 12–14.

1899 *Proboscina crassa* (Roemer) var. *divaricata* d'Orbigny; Gregory: 35; pl. 2, fig. 8.

MATERIAL. BM(NH) 60538, Cunnington Colln (figd as *Proboscina crassa* (Roemer) var. *divaricata* (d'Orbigny) by Gregory, 1899: pl. 2, fig. 8); D5150 (2 specimens), D5151, Cunnington Colln; D6325, A. N. Davies Colln; D7982–3, Treacher Colln; D55319, Little Coxwell Pit, Gaster Colln; D55320, Bowler's Pit, Gaster Colln (questionably assigned to this species); D55412, Little Coxwell Pit, Taylor Colln.

DESCRIPTION. Zoarium adnate, with narrow multiserial, ribbon-like branches, generally 2–3 autozooecia in width, bifurcating irregularly and, less commonly, giving rise to lateral branches at right angles. Branches are low and flat, sometimes anastomosing, with a gently tapering selvedge of narrow kenozooecia (visible in wetted specimens).

Autozooecia are elongate, with small circular apertures a variable but large distance apart, and usually have short peristomes, though peristomes up to 0·3 mm have been observed; frontal walls are ornamented by rounded diamond-shaped pseudopores, about 1000 per mm^2.

MEASUREMENTS. TAM, 0·10–0·14 mm (mean 0·12 mm); TPM, 0·20–0·24 mm (mean 0·23 mm); FWL, 0·90–1·20 mm; FWW, mean 0·30 mm; BW, 0·50–1·00 mm.

REMARKS. The Faringdon material agrees well with d'Orbigny's original description of *P. marginata* from the Aptian of Les Croûtes (Aube), which emphasizes the presence of marginal kenozooecia ('cellules bordées'). Although d'Orbigny (1853) found an ancestrula from Les Croûtes, ancestrulae have not been observed in Faringdon specimens, with the exception of a small colony (BM(NH) D55320) tentatively assigned to *P. marginata* but not developing the characteristic selvedge of kenozooecia (which is possibly a late astogenetic feature, cf. Illies 1981). In this colony the protoecium is large (0·24 mm transverse diameter), and the ancestrula is 0·38 mm long with an aperture 0·09 × 0·08 mm; the earliest branch division occurs at a high angle.

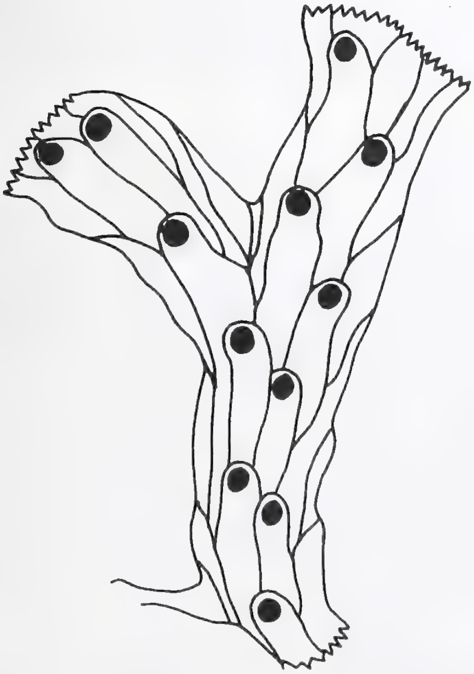


Fig. 17 Drawing of part of a branch of *Proboscinopora marginata* (d'Orbigny) in specimen BM(NH) D7982 showing the medial autozooecia and marginal kenozooecia whose outlines are visible when the specimen is immersed in water; × 21; see also Fig. 16.

Pergens (1889) regarded *P. marginata* and *P. ricordeauana* d'Orbigny, 1853 as conspecific, but this opinion seems unlikely on the basis of d'Orbigny's figures. Pergens also stated that d'Orbigny's specimens of these two species were worn, but this contradicts d'Orbigny's figures and suggests that Pergens may not have had d'Orbigny's original figured material at hand.

Faringdon specimens are usually found encrusting phosphatic or quartzose pebbles.

Stomatoporid sp. 1 Fig. 18

MATERIAL. BM(NH) D55115, Little Coxwell Pit, Gaster Colln; D55363, Little Coxwell Pit, Pitt Colln.

DESCRIPTION. Zoarium with branches of uniserially-arranged zooecia; new branches arise laterally, almost at right angles to the parent branch and about midway along a zooecium in the parent branch. Zooecia are extremely long and narrow; apertures are very small with no significant peristomes preserved. Pseudopores are not visible in the poorly-preserved specimens available. The ancestrula is unknown.

MEASUREMENTS. TAM, 0·07 mm; TPM, 0·14 mm; FWL, 0·6–1·0 mm; FWW, 0·16 mm.

REMARKS. This apparently undescribed species is represented by only two very poorly-preserved and fragmentary specimens, one (D55115) encrusting an oyster and the other (D55363) a sponge. The slender zooecia and lateral branching are quite characteristic, but in view of the preservation and absence of early growth stages it would be unwise to establish a new species.

In size and shape the zooecia resemble *Stomatopora longiscata* d'Orbigny (1853: pl. 629, figs 9–11), from the Cenomanian of northern France, which from d'Orbigny's figure appears to have a pattern of lateral branching. However, Pergens (1889) revised d'Orbigny's type of *S. longiscata* and showed the branching pattern to be dichotomous; the Faringdon species is therefore not regarded as conspecific with *S. longiscata*.

Lateral branching is a characteristic of *Voigtopora* among stomatoporids. Unlike the present Faringdon stomatoporid, however, species of *Voigtopora* have broad zooecia with long proximal prolongations flanking the next proximal zooecium in series (see p. 70). Generic attribution of the present species is therefore equivocal.

Stomatoporid sp. 2 Fig. 19

MATERIAL. BM(NH) D55106 (with *Plagioecia orbifera* and *'Berenicea' faringdonensis*), Little Coxwell Pit, Gaster Colln; D57596, Wicklesham Pit, Wilson Colln; D57724, Little Coxwell Pit, Elliott Colln; D57725, Little Coxwell Pit, Pitt Colln.

DESCRIPTION. Zoarium with branches of uniserially arranged zooecia. Branches bifurcate frequently, commonly at angles of about 90°, but varying between 45° and 100°. Internodes comprise between one and four zooecia, many having one or two zooecia. Early astogeny is unknown. Zooecia are small and slender, typically at their narrowest proximally.

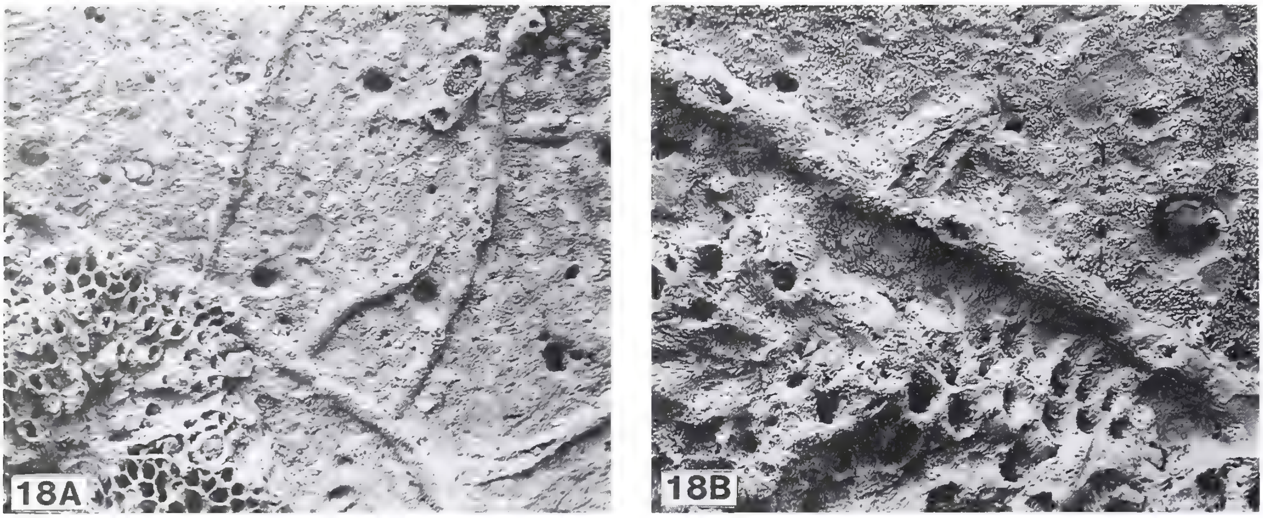


Fig. 18 Stomatoporid sp. 1, BM(NH) D55115; 18A, branches with lateral ramifications, × 14; 18B, elongate zooecia, × 40.

Apertures are small, and peristomes of significant length have not been observed.

MEASUREMENTS. FWL, 0·39–0·51 mm; FWW (distal), 0·09–0·15 mm; FWW (proximal), 0·03–0·05 mm.

REMARKS. Most of the available material of this species is fragmentary and poorly-preserved, with surface detail obscured by calcite cement or a ferruginous coating. The species is, however, clearly distinguishable from 'Stomatoporid sp. 1' by its smaller zooecia and bifurcating branches.

Family **ONCOUSOECIIDAE** Canu, 1918

Genus ***ONCOUSOECIA*** Canu, 1918

TYPE SPECIES. *Tubulipora lobulata* Hincks, 1880 (=*Alecto dilatans* Johnston, 1847; see Hastings 1963), by original designation; Recent.

REMARKS. It was common practice for early palaeontologists (e.g. Gregory 1896, 1899) to assign all tubuliporinid species with ribbon-like encrusting colonies (probosciniform) to the Recent genus *Proboscina* Audouin (see above, p. 74). Several Mesozoic species of '*Proboscina*' possess gynozooecia (e.g. Walter 1970) which resemble those of the Recent type species of *Oncousoecia*. The gynozooecium in *Oncousoecia* is typically small, has a longitudinally elongate distal part and a transversely elliptical ooeciopore a little smaller than an autozooecial aperture.

RANGE. Aalenian to Recent.

Oncousoecia coarctata (Canu & Bassler, 1926)

Figs 20–22

1926 *Proboscina coarctata* Canu & Bassler: 8; pl. 28, fig. 1.

1926 *Proboscina ricordeauana* (d'Orbigny); Canu & Bassler: 7; pl. 27, figs 7–8.

1986 '*Proboscina coarctata*' Canu & Bassler; Wilson: 693.

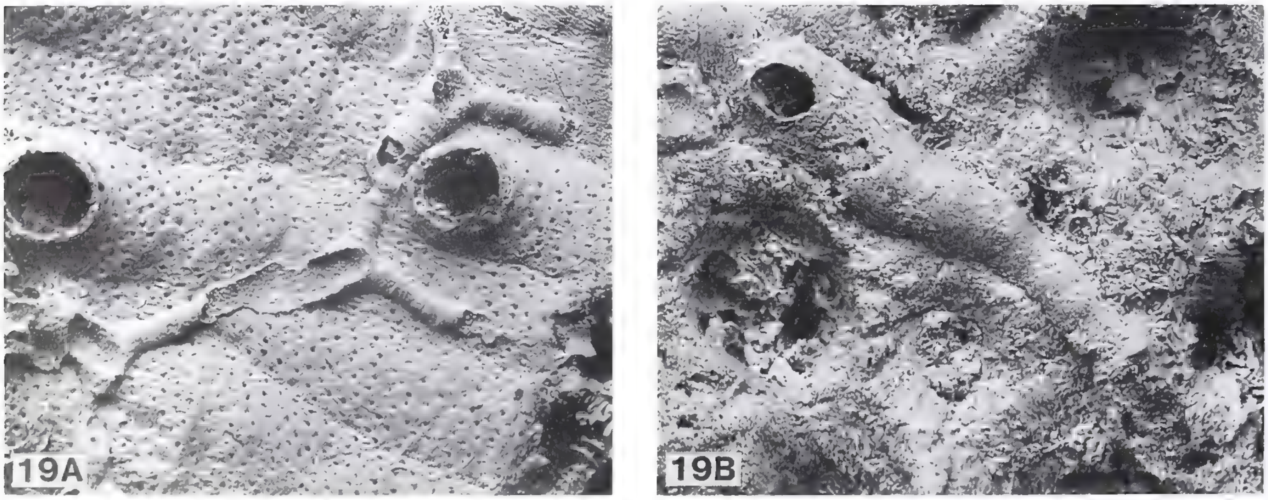
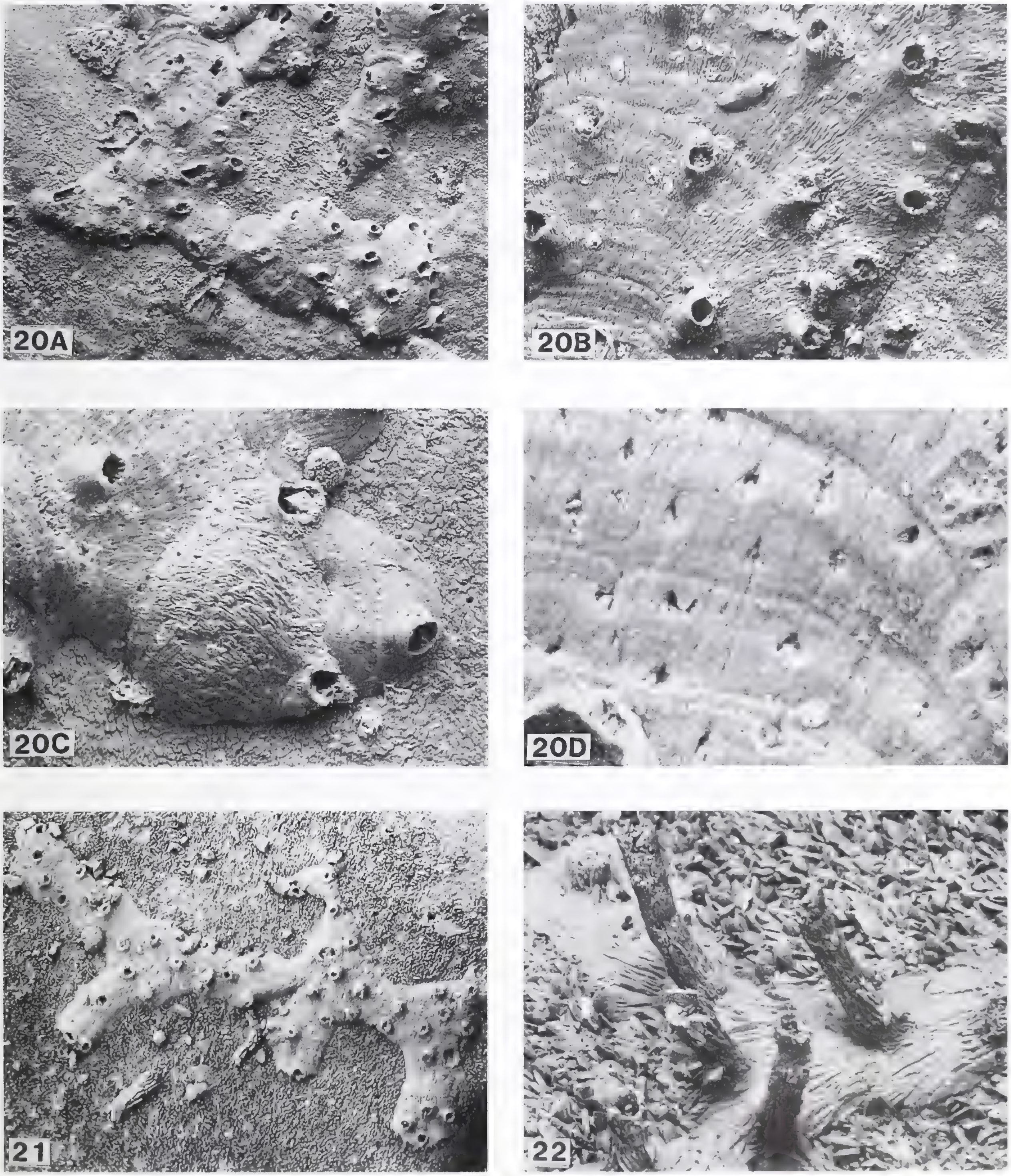


Fig. 19 Stomatoporid sp. 2, BM(NH) D55106; 19A, abraded zooecia overgrowing '*Berenicea*' *faringdonensis*, × 79; 19B, well-preserved zooecium, × 142.



Figs 20–22 *Oncousoecia coarctata* (Canu & Bassler). Fig. 20, USNM 69000, holotype; 20A, fractured lobate branches, × 26; 20B, autozooecia, × 73; 20C, gynozooecium, × 100; 20D, autozooecial pseudopores, × 400. Fig. 21, BM(NH) D55095, small colony, × 17. Fig. 22, BM(NH) D55094, exceptionally long peristomes, × 78.

HOLOTYPE. USNM 69000, figd by Canu & Bassler (1926: pl. 28, fig. 1).

OTHER MATERIAL. BM(NH) 60537 (with *Voigtopora calypso*); D6326 (with *'Stomatopora' melvillei*), A. N. Davies Colln; D55094–5, D55189–90, D57393, D57395, Little Coxwell Pit, Pitt Colln; D55188, Bowler's Pit, Pitt Colln; D55432, D55434 Wicklesham Pit, Wilson Colln.

DESCRIPTION. Colony adnate, consisting of narrow oligoserial branches usually between 2 and 8 zooecia wide, sometimes flabellate. Branches have a characteristically low relief and flat surface. Branch division is normally dichotomous at angles between 60° and 80°, but branches occasionally trifurcate. Episodic growth is suggested by the occurrence of flabellate branches with rounded distal margins from which proximally constricted daughter branches arise; apparent severing of one such daughter branch from its parent is observable in the holotype. Ancestrulae are rarely preserved; in specimen BM(NH) D57395 the ancestrula is 0·23 mm long and has a protoecium 0·14 mm in transverse diameter.

Autozooecia are small, slender, immersed (i.e. their frontal outlines are poorly visible) and sometimes have a transversely wrinkled frontal wall. Pseudopores are sparse (750–900 per mm^2.) and dart-shaped (Fig. 20D). Apertures are widely spaced, small, circular or transversely elliptical, usually with a thin-walled, low peristome; however, peristomes up to 0·45 mm long are preserved in a recess in specimen BM(NH) D55094 (Fig. 22).

Gynozooecia (Fig. 20C) are small, orbicular, slightly longer than wide, and have a terminal ooeciopore which is a little smaller than an autozooecial aperture.

MEASUREMENTS. LAM, 0·06–0·09 mm; TAM, 0·06–0·09 mm; FWL, 0·59–0·74 mm; FWW, 0·14–0·15 mm; GDL, 0·32–0·40 mm; GW, 0·25–0·39 mm; LOPM, 0·05 mm; TOPM, 0·06 mm; BW, 0·27–0·90 mm.

REMARKS. Unfortunately, Canu & Bassler (1926) chose an exceptional specimen as their type of *Proboscina coarctata*. This specimen has strongly flabellate branches (Fig. 20A), constricted at intervals and giving rise to daughter branches, and lacks the dichotomously branching pattern of most apparently conspecific specimens from Faringdon. The gynozooecia (Fig. 20C) present in this specimen apparently went unnoticed by Canu & Bassler.

The *Proboscina ricordeauana* d'Orbigny of Canu & Bassler (1926) appears identical to *P. coarctata*, and is unlike true *P. ricordeauana* d'Orbigny in which the branches are more convex. According to Pergens (1889), *P. ricordeauana* is probably conspecific with *P. marginata* (see p. 74), an opinion not supported by d'Orbigny's (1853) figures of the two species.

O. coarctata is a common species at Faringdon and can be found encrusting a variety of substrates including phosphatic pebbles, oyster shells and sponges.

Oncousoecia parvula (Canu & Bassler, 1926)

Figs 23–24

1926 *Berenicea parvula* Canu & Bassler: 10; pl. 28, figs 8–9.
1926 *Microecia cornucopia* (d'Orbigny); Canu & Bassler: 37; pl. 28, figs 5–7.
1926 *Proboscina virgula* (d'Orbigny); Canu & Bassler: 8; pl. 27, figs 9–10.
1986 *'Proboscina'* sp. B; Wilson: pl. 53, fig. 3.

MATERIAL. BM(NH) D52200 (8 specimens), D55180, Little Coxwell Pit, Pitt Colln; D55124 (with *Idmonea denticulata* and *Reptoclausa hagenowi*), Little Coxwell Pit, Gaster Colln; D55179, Little Coxwell Pit, Curry Colln; D53225 (with *Stomatoporina alternata*), Little Coxwell Pit, Taylor Colln; D55181, D57425–6, Little Coxwell Pit, Thomas Colln; D55422 (figd as *'Proboscina'* sp. B by Wilson 1986: pl. 53, fig. 3), D55435, Wicklesham Pit, Wilson Colln. USNM 69837 (figd as *Proboscina virgula* (d'Orbigny) by Canu & Bassler 1926: pl. 27, figs 9–10); 69882 (figd as *Microecia cornucopia* (d'Orbigny) by Canu & Bassler 1926: pl. 28, figs 5–7).

DESCRIPTION. Colony adnate, consisting of narrow (up to 0·90 mm wide), oligoserial branches (Fig. 24A), seldom bifurcating, usually 3–5 zooecia wide, sometimes flabellate, and flat to slightly convex in cross section.

Autozooecia are very small, visible for most of their length, with transversely wrinkled, convex frontal walls (Fig. 24C). Apertures are small, longitudinally elongate, arranged roughly in quincunx and are closely-spaced with moderately raised peristomes.

Gynozooecia (Figs 23B, 24D) are small, with an orbicular distal part which may be bulbous. The ooeciopore is terminal and slightly transversely elongated, a little larger than an autozooecial aperture, with a prominent but short ooeciostome.

MEASUREMENTS. LAM, 0·06–0·08 mm; TAM, 0·04–0·06 mm; FWL, 0·20–0·36 mm; FWW, 0·09–0·12 mm; GDL, 0·50 mm; GW, 0·30 mm; LOSM, 0·08 mm; TOSM, 0·12 mm.

REMARKS. This species was originally described by Canu & Bassler (1926) as *Berenicea parvula*, although their description and figures clearly indicate that the colony-form of their material was probosciniform rather than bereniciform. The type specimen of *B. parvula* is apparently missing from the collections of the USNM; a specimen bearing the registration number of the type (USNM 69842) belongs to a different species with much larger zooecia.

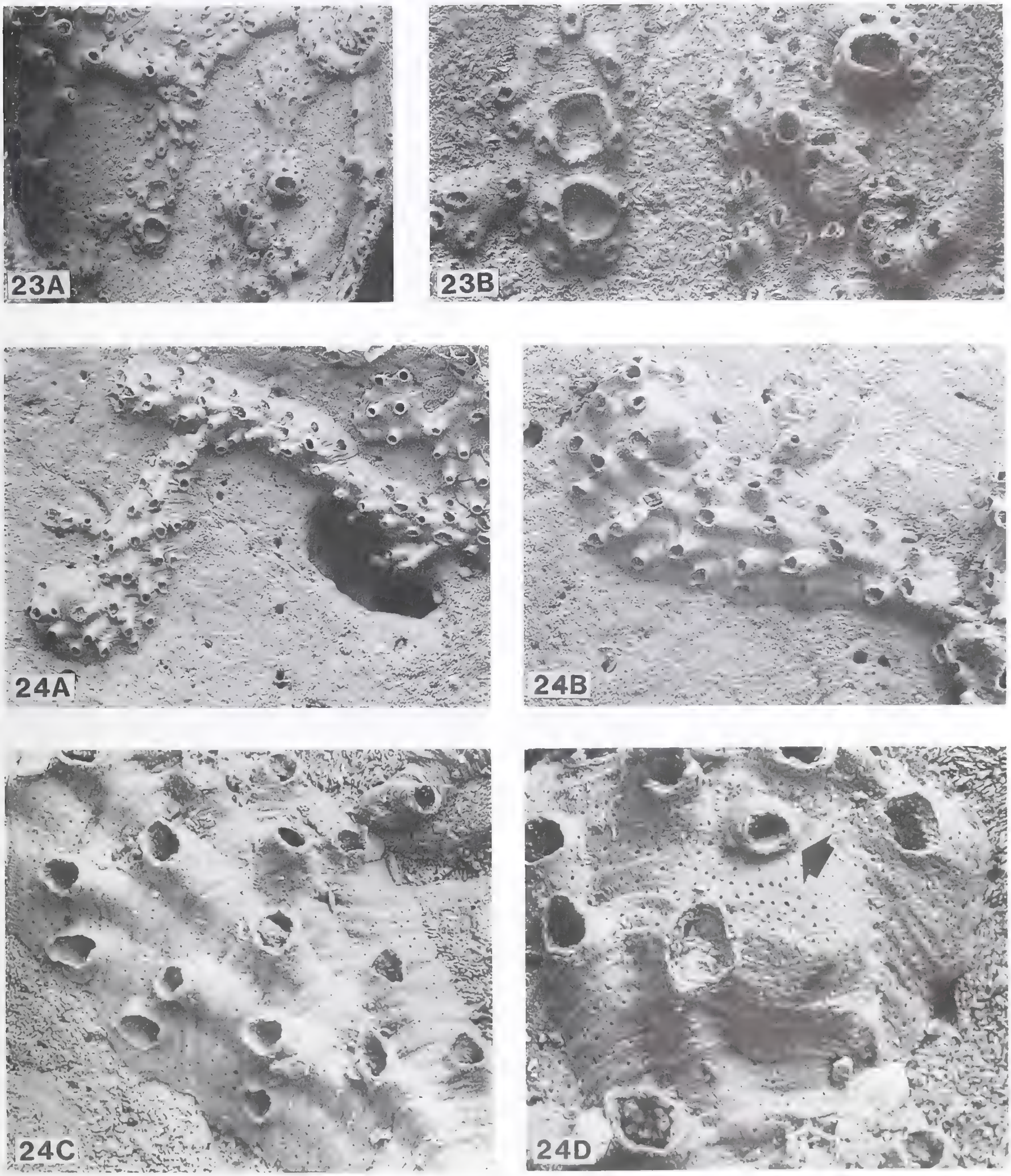
The *Microecia cornucopia* (d'Orbigny) of Canu & Bassler (1926), here synonymized with *O. parvula*, is not conspecific with d'Orbigny's species which is from the Upper Cretaceous of France. D'Orbigny's figures (1853: pl. 634, figs 7–9) are comparatively uninformative, but Gregory (1899) described some British Upper Cretaceous specimens as *P.cornucopia* which resemble the specimens figured by d'Orbigny. These specimens are not conspecific with *O. parvula*, which has narrower and less clearly flabellate branches and smaller zooecia. Canu & Bassler (1926) also mis-assigned specimens of *O. parvula* to *Proboscina virgula* (d'Orbigny), a Cenomanian species with branches distinctly subtriangular in cross-sectional shape (see d'Orbigny 1853: pl. 631, figs 15–17).

Specimens of *O. parvula* occur as small, delicate colonies mostly encrusting fragments of bivalves, brachiopods and other bryozoans.

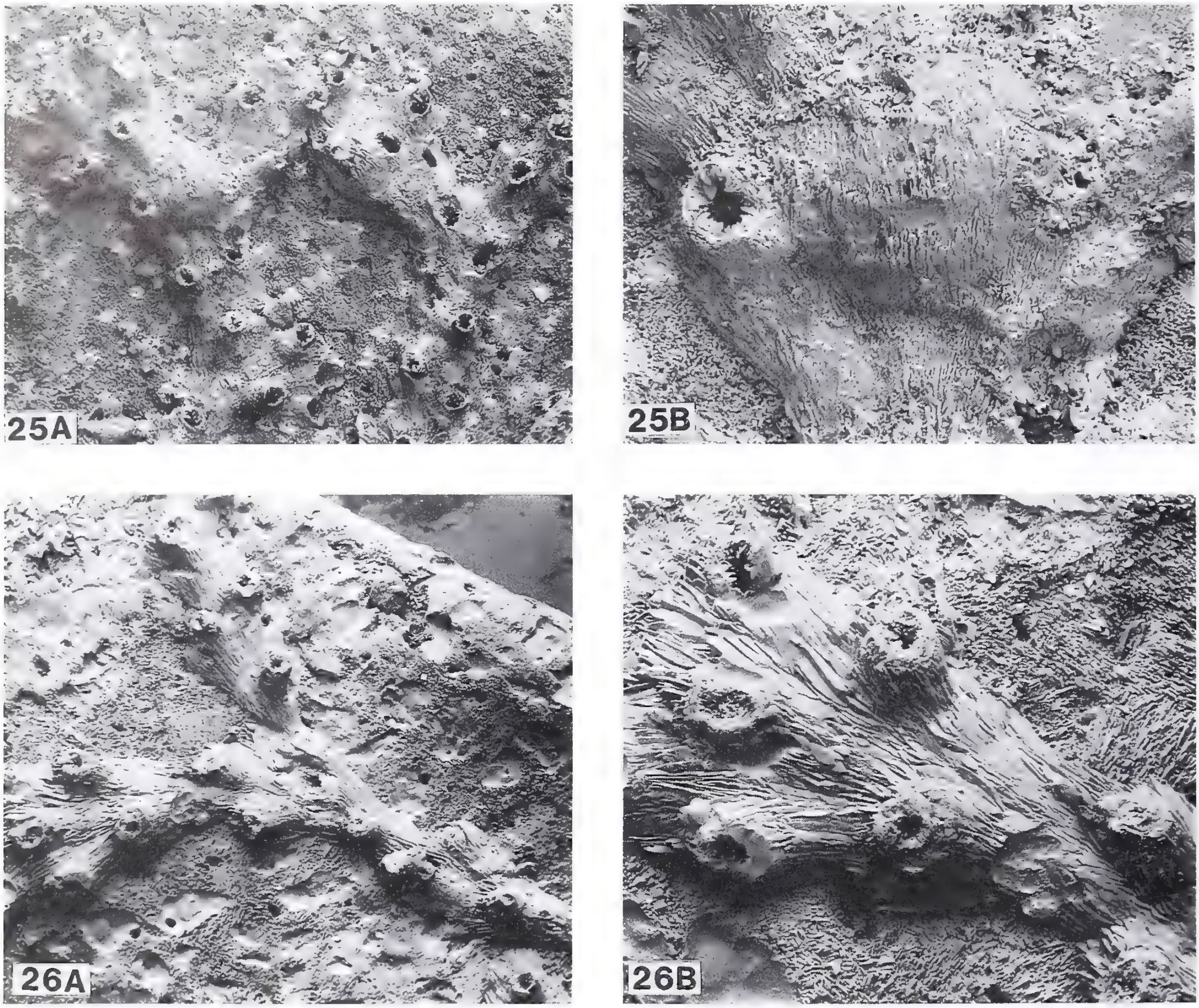
Oncousoecia depressa (d'Orbigny, 1850, *sensu* Canu & Bassler, 1926)

Figs 25–26

?1850 *Idmonea depressa* d'Orbigny: 109.
?1853 *Proboscina depressa* (d'Orbigny) d'Orbigny: 849; pl. 631, figs 12–14.
1926 *Proboscina depressa* (d'Orbigny); Canu & Bassler: 8; pl. 27, figs 5–6.



Figs 23–24 *Oncousoecia parvula* (Canu & Bassler). Fig. 23, BM(NH) D55422; 23A, colony branches encrusting the interior of a bivalve boring along with *Stomatopora*, × 16; 23B, numerous gynozooecia in two branches growing in opposite directions, × 35. Fig. 24, BM(NH) D55124: 24A, × 27; 24B, × 41; 24C, autozooecia, × 99; 24D, gynozooecium with ooeciopore arrowed, × 130.



Figs 25–26 *Oncousoecia depressa* (d'Orbigny, *sensu* Canu & Bassler). Fig. 25, BM(NH) D57430; 25A, × 19; 25B, gynozooecium (ooeciopore apparently obscured by calcite cement), × 48. Fig. 26, BM(NH) D55313; 26A, × 21; 26B, coarsely-preserved autozooecia, × 50.

MATERIAL. BM(NH) D55313, Little Coxwell Pit, Gaster Colln; D57430, Little Coxwell Pit, Pitt Colln. USNM 69483 (figd by Canu & Bassler, 1926: pl. 27, figs 5–6).

DESCRIPTION. Zoaria are encrusting, initially uniserial but becoming oligoserial, with somewhat flabellate branches, 2–3 zooecia wide, which bifurcate frequently. Branches are relatively flat and low.

Autozooecia are moderately large but of variable size, with slightly convex frontal walls visible for most of their length. Apertures are circular or longitudinally elliptical and widely spaced, and peristomes are little raised.

Gynozooecia (Fig. 25B) have small, inverted pear-shaped distal frontal walls and a transversely elongate ooeciopore.

MEASUREMENTS. LAM, 0·11–0·15 mm; TAM, 0·12–0·15 mm; FWL, 0·86–1·07 mm; FWW, 0·21–0·30 mm; GW, 0·50 mm; GDL, 1·10 mm; TOSM, 0·08 mm; LOSM, 0·04 mm; TOPM, 0·04 mm; LOPM, 0·03 mm.

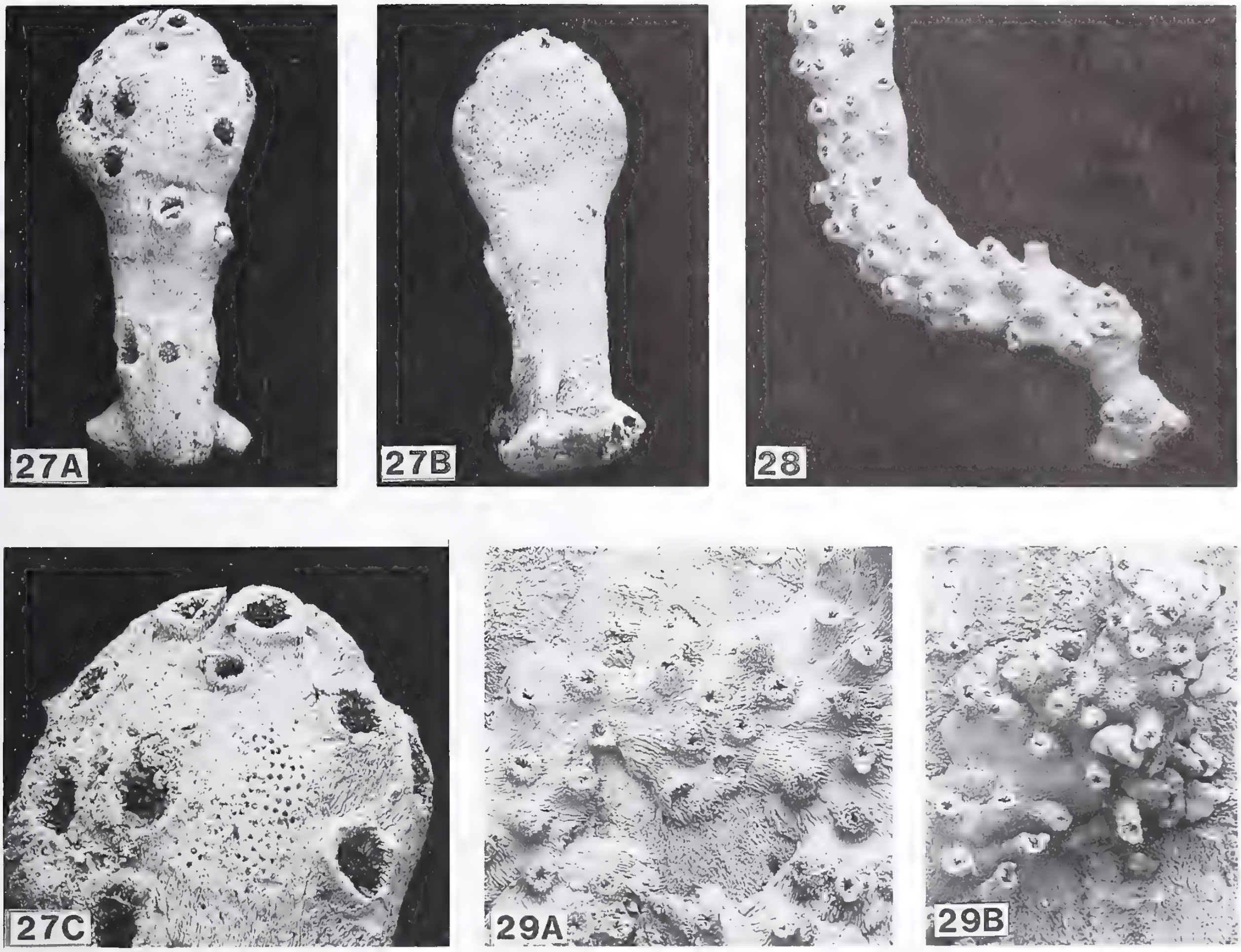
REMARKS. D'Orbigny (1850, 1853) described a species from the Neocomian of France which Canu & Bassler (1926) later identified from Faringdon under the name *Proboscina depressa* (d'Orbigny). However, it is difficult to be certain that the French and Faringdon specimens are conspecific in view of the relatively undistinctive morphology of the species and the absence of a revision of d'Orbigny's type material; Pergens (1889) merely records the occurrence of a worn colony in the d'Orbigny Collection. Therefore, the Faringdon material is here redescribed as *depressa, sensu* Canu & Bassler, 1926.

The gynozooecia and low profile of the branches allow generic assignment to *Oncousoecia*. The species can be distinguished from other Faringdon species of *Oncousoecia* by its larger zooecia.

Genus ***FILISPARSA*** d'Orbigny, 1853

TYPE SPECIES. *Filisparsa neocomiensis* d'Orbigny, 1853, by subsequent designation of Gregory, 1899; Neocomian, France.

REMARKS. *Filisparsa* is an oncousoeciid in which colonies develop erect branches with autozooecia opening only on the obverse surfaces of branches; reverse surfaces comprise exterior basal walls of the autozooecia. Walter (1972) regarded the type species, *F. neocomiensis* d'Orbigny, as an erect form of



Figs 27–29 *Filisparsa gasteri* sp. nov. Fig. 27, BM(NH) D55379, **holotype**; 27A, obverse side of branch, × 25; 27B, reverse side of branch, × 23; 27C, gynozooecium, × 70. Fig. 28, BM(NH) D55381, branch obverse, × 18. Fig. 29, BM(NH) D57427, colony base; 29A, encrusting zooecia, × 24; 29B, base of erect stem, × 20.

Stomatopora granulata (Milne Edwards), and therefore rejected the genus *Filisparsa*.

Gynozooecia have apparently not been described in *F. neocomiensis*, but the occurrence of ovoidal gynozooecia in *F. gasteri* sp. nov. (see below) and in several Upper Cretaceous species assigned to *Filisparsa* by Brood (1972), implies that *Filisparsa* is not a stomatoporid. Brood (1972) proposed a new family, Filisparsidae, with *Filisparsa* as type genus. This was necessary because he did not accept the family Oncousoeciidae. The Filisparsidae is here regarded as synonymous with the Oncousoeciidae.

Hinds (1975) described the mode of growth of *Filisparsa* and similar genera, noting that the diagnosis of the genus is broad and *Filisparsa* may be polyphyletic.

RANGE. Lower Cretaceous (Neocomian) to Recent.

Filisparsa gasteri sp. nov. Figs 27–29

HOLOTYPE. BM(NH) D55379, Little Coxwell Pit, Pitt Colln.

PARATYPES. BM(NH) D55380, Little Coxwell Pit, Thomas Colln; D55381, D55383, Little Coxwell Pit; D55382, D57427, Little Coxwell Pit, Pitt Colln; D55384, D55385, Little Coxwell Pit, Elliott Colln; D55386, Little Coxwell Pit, Taylor Colln.

NAME. For Christopher T. A. Gaster, who presented his large collection of Cretaceous invertebrates, including many Bryozoa, to the BM(NH) in 1938 and 1950.

DESCRIPTION. Known specimens are small, the largest observed erect branch being 4·3 mm high and 0·70 mm wide (BM(NH) D55381). Erect branches are compressed and have an obverse surface bearing autozooecial apertures in 3–4 rows, and a flat reverse surface comprising the exterior basal walls of the autozooecia (Fig. 27B); they have not been observed to bifurcate. Branch edges may be smooth or may have a serrated appearance due to the projecting peristomes of the marginal zooecia. The encrusting base (Fig. 29) is fairly extensive and consists of bifurcating oligoserial branches about 3–4 zooecia in width; several erect branches may arise from the colony base, each formed by the upturning of the distal end of an encrusting branch.

Autozooecia are variable in length and have elongate, slightly convex frontal walls, small circular to longitudinally elongate apertures, and moderately raised peristomes.

Gynozooecia (Fig. 27C) are borne on the erect branches, and are very small with longitudinally ovate dilated distal frontal walls, very short proximal frontal walls, and a small transversely elliptical ooeciopore.

MEASUREMENTS. TAM, 0·08–0·10 mm; FWL, 0·27–0·50 mm;

FWW, 0·17–0·20 mm; GTL, *c.* 0·78 mm; GW, *c.* 0·34 mm; LOSM, *c.* 0·08 mm; TOSM, *c.* 0·10 mm; LOPM, *c.* 0·05 mm; TOPM, *c.* 0·06 mm.

REMARKS. This uncommon species differs from *F. neocomiensis* d'Orbigny by having more closely-spaced apertures (see d'Orbigny 1853: pl. 760, figs 10–13), and lacking the distinct cresent-shaped growth lines depicted by d'Orbigny on branch reverse surfaces. However, a precise evaluation of the distinctions and relationships between the two species must await a modern revision of d'Orbigny's type specimens.

Family **MULTISPARSIDAE** Bassler, 1935
(= MACROECIIDAE Canu, 1918)

Genus ***REPTOCLAUSA*** d'Orbigny, 1853

TYPE SPECIES. *Reptoclausa neocomiensis* d'Orbigny, 1853, by subsequent designation of Bassler, 1935; Valanginian of Ste Croix (Switzerland).

REMARKS. The type species of *Reptoclausa* has been revised by Hillmer (1971). The genus is distinguished by its characteristic colony form; colonies are sheet-like and have autozooecia located on ridges which form subcolonies separated by expanses of kenozooecia. *Reptoclausa* appears to be closely related to *Idmonea* (see below, p. 84). The autozooecial ridges may be homologous with the branches of the latter genus, and the kenozooecia equivalent to the kenozooecia which often form a selvedge on the flanks of the branches of *Idmonea*.

Species of *Reptoclausa* differ from one another in the shapes and relationships of the autozooecial ridges. In *R. neocomiensis* the ridges are short and taper both distally and proximally; new ridges arise from areas of kenozooecia and are not connected with established ridges. A similar arrangement occurs in *R. hagenowi* (see below), but the ridges are typically longer. Furthermore kenozooecia in *R. hagenowi* are extremely slender, whereas those of *R. neocomiensis* have hexagonal frontal walls only slightly smaller in area than the autozooecial frontal walls. A Jurassic species of *Reptoclausa*, *R. porcata* Taylor, 1980, has kenozooecia which resemble those of *R. hagenowi*, but the autozooecial ridges are more rounded in profile and new ridges arise by the bifurcation of established ridges.

RANGE. Aalenian to Maastrichtian.

Reptoclausa hagenowi (Sharpe, 1854) Figs 30–33

1854 *Lopholepis hagenovii* [sic] Sharpe: 196; pl. 5, fig. 7a–d.
1899 *Idmonea hagenowi* (Sharpe) Gregory: 150; pl. 8, figs 1a–b.
1926 *Reptoclausa hagenowi* (Sharpe) Canu & Bassler: 82; pl. 18, figs 2–5.
1981 *Reptoclausa neocomiensis* d'Orbigny; Voigt: fig. 1i.
1986 *Reptoclausa hagenowi* (Sharpe); Wilson: pl. 53, fig. 9.

LECTOTYPE. BGS 7560, Sharpe Colln, designated herein as lectotype.

PARALECTOTYPE. BGS 7561, Sharpe Colln.

OTHER MATERIAL. BM(NH) 55110 (figd by Gregory 1899: pl. 8, fig. 1a, b); 51164, J. Sharp Colln; D3026, D3139, D50392, ?Colln; D3140, D3141, Charlesworth Colln; D4503 (4), Cunnington Colln; D7166, Ellis Colln; D50391, Wicklesham Pit, Pitt Colln; D52185–6, Little Coxwell Pit, Pitt Colln; D55118, D55124 (with *Oncousoecia parvula* and *Idmonea denticulata*), D55322–3, Little Coxwell Pit, Gaster Colln; D55119, Gaster Colln; D55321 (12), D57436, Little Coxwell Pit, Cleevely Colln; D55324, ?Little Coxwell Pit, Cleevely Colln; D55420 (figd by Wilson 1986: pl. 53, fig. 9), D55434, Wicklesham Pit, Wilson Colln; D57433–4, Little Coxwell Pit, Thomas Colln; D57435, Hinde Colln.

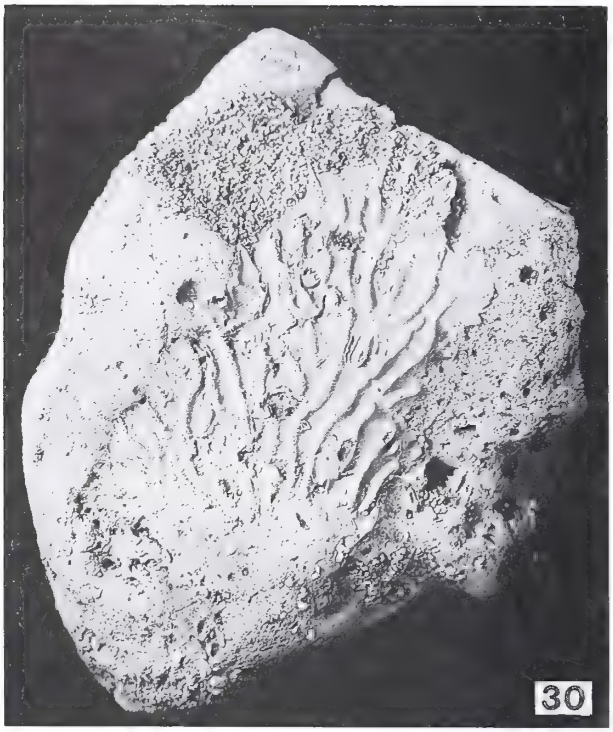
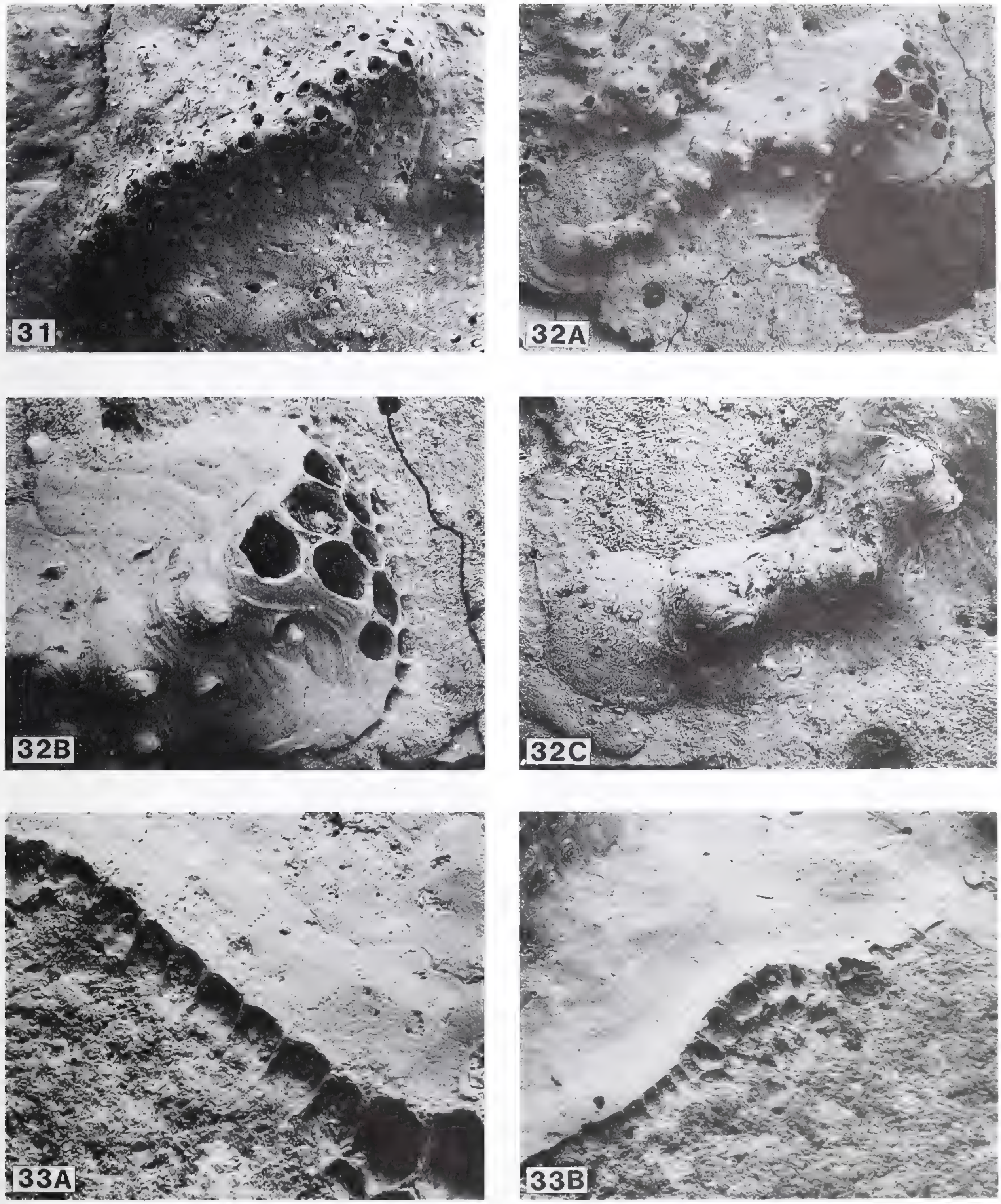


Fig. 30 *Reptoclausa hagenowi* (Sharpe), BM(NH) D50391, optical photograph of large colony encrusting a cobble, × 1·5.

DESCRIPTION. Zoarium adnate, sheet-like, with ridges composed of autozooecia forming elongate subcolonies (up to 12 mm long by 0·6–0·8 mm wide) separated by depressed areas of kenozooecia (Fig. 30). Autozooecial ridges may be sinuous. New ridges arise at the growing edge between existing ridges (i.e. individual subcolonies are not in continuity with one another), and ridges may taper in height and width and disappear distally. Zoaria are very thin and their surfaces are featureless between ridges.

The ancestrula has a large protoecium (diameter 0·35 mm) and a short distal tube (0·45 mm) which bends to one side (Fig. 32C). Early post-ancestrular zooecia also bend, some to the right and some to the left. Young colonies are V-shaped wedges (Fig. 32A) and consist of a single autozooecial ridge increasing in elevation distally and flanked by a selvedge of kenozooecia. During later growth the ancestrula is overgrown, and new autozooecial ridges are added in orientations approximately at right angles to the initial autozooecial ridge.

Autozooecia are immersed, have slight peristomes and subcircular apertures which are sometimes occluded by terminal diaphragms, especially in autozooecia at the bases of

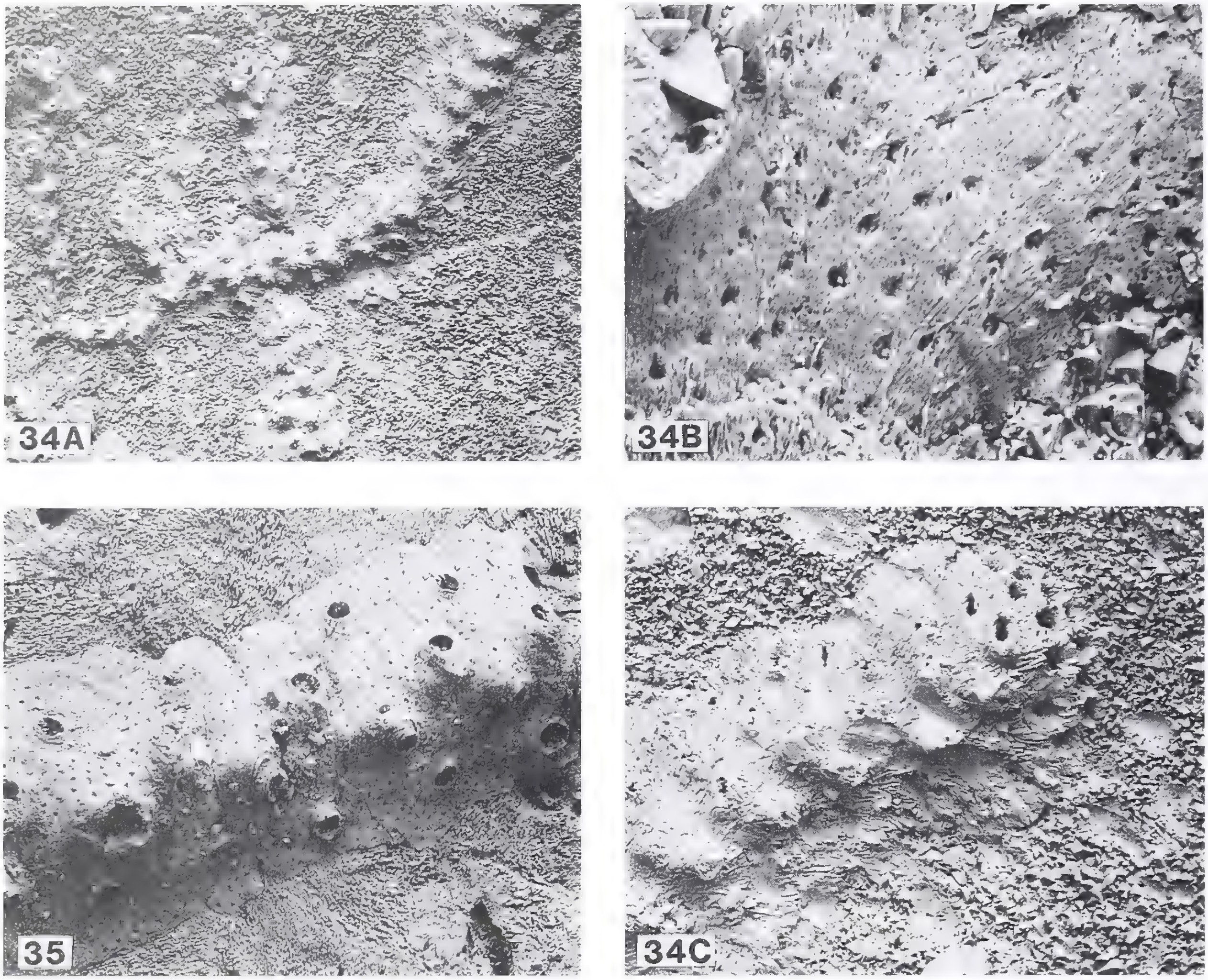


Figs 31–33 *Reptoclausa hagenowi* (Sharpe). Fig. 31, BM(NH) D55119, ridge of autozooecia, ×15. Fig. 32, BM(NH) D55124, small colony: 32A, × 19; 32B, growth margin, × 43; 32C, ancestrula (with large protoecium) and early budded zooecia, all with apertures turned to the right, × 81. Fig. 33, BM(NH) D55118; 33A, kenozooecial buds at the growth margin, ×120; 33B, newly-forming autozooecial ridge, × 31.

the ridges adjoining the regions of kenozooecia. Apertural diameter characteristically increasing from the base to the crest of the ridges, and apertures on either side of the ridge crest are arranged in alternating rows. About 1600 pseudopores per mm^2 occur on autozooecial frontal walls.

Kenozooecia are immersed, poorly defined, and have slender frontal walls; they are most easily visible as tiny buds at the growing edge between the autozooecial ridges (Fig. 33A).

Gynozooecia are situated on ridge crests, may be very



Figs 34–35 *Idmonea denticulata* (Canu & Bassler). Fig. 34, USNM 69936, holotype; 34A, early parts of colony with lateral branch ramifications, × 17; 34B, autozooecial pseudopores, × 340; 34C, growth tip, × 39. Fig. 35, BM(NH) D55124, × 58.

inconspicuous and are usually abraded. They have a longitudinally elliptical shape with a minute ooeciopore.

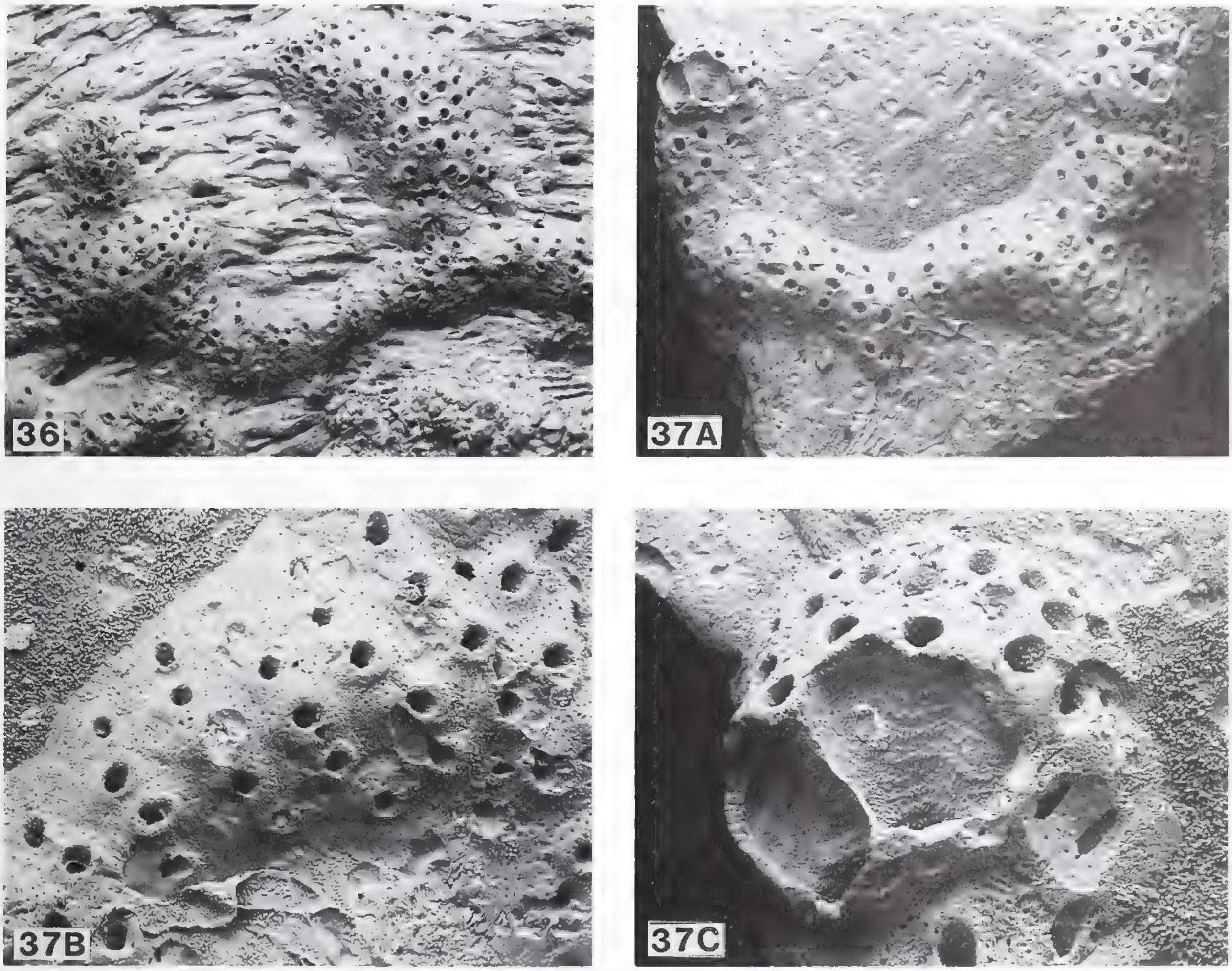
Measurements. TAM (top of ridges), 0·10–0·12 mm; TAM (sides of ridges), 0·06–0·08 mm; GDL, *c.* 1·0 mm; GW, *c.* 0·75 mm.

Remarks. This is a very common and distinctive species at Faringdon. Colonies are often found encrusting quartzose or claystone pebbles (e.g. Fig. 30), but may also occur on bivalve shells and sometimes on brachiopods and echinoid spines. Wilson (1986) interpreted *R. hagenowi* as being well-adapted to the physically rigorous habitats afforded by the exteriors of claystone pebbles in the Red Gravels. However, the robust construction of the colonies may also have contributed to their occurrence in this habitat. Indeed, many specimens of *R. hagenowi* evidently survived extensive abrasion, probably post-mortem, which often resulted in truncation of the ridge crests.

Genus ***IDMONEA*** Lamouroux, 1821.

Type species. *Idmonea triquetra* Lamouroux, 1821, by monotypy; Bathonian, Normandy (see Mongereau & Walter 1965; Walter 1970).

Remarks. *Idmonea* has been used by Mesozoic palaeontologists in a way different from neontologists. The latter have commonly referred erect tubuloporine species with branches of a subtriangular cross section to this genus (but cf. Harmelin 1976). However, the Jurassic type species is a tubuloporine with encrusting branches, subtriangular in cross section and with a selvedge of kenozooecia which does not coalesce with that of other branches to form a continous sheet (cf. *Reptoclausa*). 'Adventitious' branches sometimes originate from the kenozooecial selvedge. From the encrusting base erect branches may arise, having an ovoidal cross-sectional shape with autozooecial apertures opening on one side of the branch and kenozooecia on the other. These erect branches



Figs 36–37 *Idmonea radiolitorum* d'Orbigny. Fig. 36, BM(NH) D55201, colony encrusting a bone, × 13. Fig. 37, BM(NH) D52199; 37A, colony encrusting a shell fragment, × 14; 37B, autozooecia, × 30; 37C, gynozooecia with worn frontal walls, × 65.

are quite unlike the erect branches of so-called *Idmonea* from the Recent. It is uncertain whether any of the numerous erect post-Mesozoic species which have been assigned to *Idmonea* really belong to this genus (see Hinds 1975 for a revision of some Tertiary species of '*Idmonea*').

RANGE. Aalenian to ?Recent.

Idmonea denticulata (Canu & Bassler, 1926)

Figs 34–35

1926 *Reptoclausa denticulata* Canu & Bassler: 82; pl. 18, fig. 1.

HOLOTYPE. USNM 69936, figd Canu & Bassler 1926: pl. 18, fig. 1.

OTHER MATERIAL. BM(NH) D50392, ?Colln; D55124 (with *Reptoclausa hagenowi* and *Oncousoecia parvula*), D55237, D55244, Little Coxwell Pit, Gaster Colln; D55233, Little Coxwell Pit, Pitt Colln; D55438, D57596, Wicklesham Pit, Wilson Colln.

DESCRIPTION. Zoarium adnate, with gently sinuous branches of subtriangular section, seldom dividing (Fig. 35). Branches are generally about 0·6 mm in width and have a narrow selvedge of kenozooecia which are often inconspicuous. New branches arise occasionally by bifurcation but more often 'adventitiously' (Fig. 34A) from the selvedge of kenozooecia at the margin of the parent branch with which they make an angle of about 90°. Branch growth tips are rounded (Fig. 34C).

Autozooecia have short frontal walls, convex distally (particularly in zooecia at branch crests) but well immersed proximally. Distal parts of zooecia close to the branch crest are turned away from the crest. Apertures are small and circular, somewhat transversely elongated; those close to the branch crest are often slightly larger than apertures immediately adjacent to the kenozooecial selvedge, where terminal diaphragms are more frequently developed. Preserved peristomes are short and diverge from the midline of the branch. Pseudopores (Fig. 34B) are teardrop-shaped, pointed distally, and occur at a density of about 1900 per mm^2.

Gynozooecia have not been observed.

MEASUREMENTS. LAM, 0·05 mm; TAM, 0·05–0·06 mm; FWL, 0·27–0·41 mm; FWW, 0·12–0·15 mm.

REMARKS. Canu & Bassler (1926) assigned this species to the genus *Reptoclausa* d'Orbigny. However, the basal selvedge of kenozooecia only surrounds the individual branches and does not occupy the area of substratum between branches in the manner of *Reptoclausa* (see p. 82).

In the absence of gynozooecia, assignment to *Idmonea* must be provisional. Gynozooecia in the type species of *Idmonea* (*I. triquetra* Lamouroux) are longitudinally elongate.

Canu & Bassler's holotype of *I. denticulata* is a poor specimen in which the 'denticulated peristomes' are apparently a result of growth of diagenetic calcite crystals. The kenozooecial selvedge of *I. alipes* Gregory, 1899, with which Canu & Bassler compared their new species, is much broader than that of *I. denticulata*. *I. triquetra*, from the Middle Jurassic, differs in having branches which bifurcate more regularly and autozooecia with slightly raised margins to their subhexagonal frontal walls.

This is a relatively rare species at Faringdon where it is found encrusting oyster shells and pebbles. It is recognizable by the rather straggly, seldom-dividing branches.

Idmonea radiolitorum d'Orbigny, 1850 Figs 36–37

1850 *Idmonea radiolitorum* d'Orbigny: 200.
1851 *Proboscina radiolitorum* (d'Orbigny) d'Orbigny: 854; pl. 633, figs 8–10.
?1853 *Proboscina ricordeauana* d'Orbigny: 850; pl. 759, figs 6–7.
1899 *Proboscina radiolitorum* (d'Orbigny); Gregory: 48; pl. 3, fig. 5.
1926 *Proboscina radiolitorum* (d'Orbigny); Canu & Bassler: 7; pl. 27, figs 1, 2.
1926 *Proboscina zic-zac* d'Orbigny; Canu & Bassler: 7; pl. 29, fig. 7.
1971 *Proboscina* cf. *radiolitorum* (d'Orbigny); Hillmer: 38; pl. 2, fig. 1.

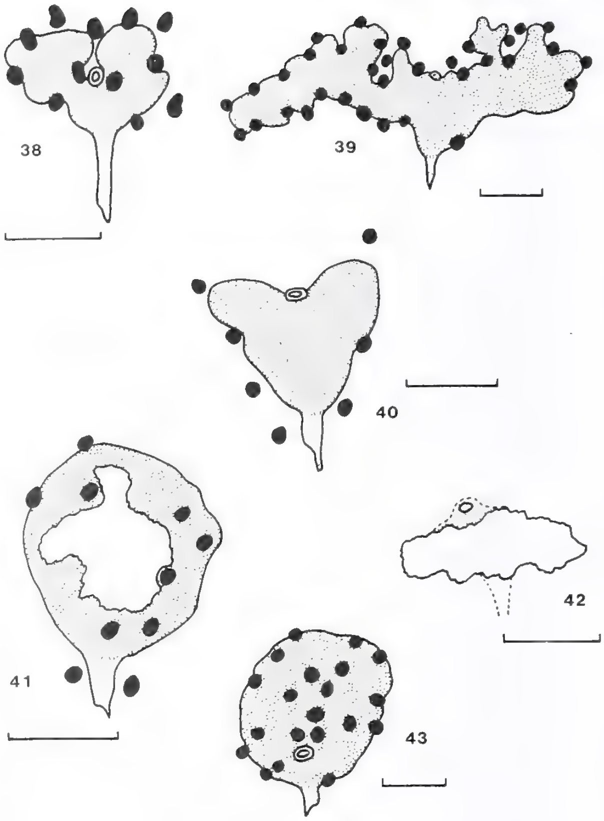
HOLOTYPE. MNHN d'Orbigny Colln 6975 (Voigt photocard 5827), Turonian, Angoulême, France.

OTHER MATERIAL. BM(NH) D7981, Treacher Colln; D52199, D52201, Little Coxwell Pit, Pitt Colln; D55240, D55243, D55244, Little Coxwell Pit, Gaster Colln; D55241 (3), Hinde Colln; D55242, D55245, Little Coxwell Pit, Thomas Colln.

DESCRIPTION. Zoarium adnate, consisting of round-topped, ribbon-like branches 4 or 5 zooecia across and 0·9–1·8 mm wide (Figs 36, 37A). Branches are typically uniform in width but may be constricted, and are often gently curved. Branching is infrequent (except during early growth stages) and occurs by bifurcation or, less often, by formation of an adventitious lateral branch almost at right angles to the parent branch. A marginal selvedge of kenozooecia is developed. Growing tips of branches are well rounded. In profile, branches are rounded and moderately high.

Autozooecia are moderately large, their frontal walls immersed and not clearly visible, especially proximally. Preserved peristomes are short but thick-walled, and apertures are of moderate size (largest in zooecia at the centre of the branches), subcircular or longitudinally elongate, and arranged in indistinct rows transverse to growth direction (Fig. 37B). Short mural spines may be visible within apertures. Pseudopores are slightly longitudinally elliptical, and occur at a density of about 1700 per mm^2.

Gynozooecia are rare but can be paired; small, bulbous, and slightly longer than wide. Short mural spines, similar to those seen in autozooecia, occur on the floor of gynozooecia (Fig. 37C). Ooeciopores have not been observed, all available gynozooecia being worn.



Figs 38–43 Gynozooecia in various species of bereniciform tubuloporines from the Faringdon Sponge Gravel. Dilated frontal walls are heavily stippled, ooeciopores are unshaded, and associated autozooecial apertures are shown in black. Scale bars represent 0·5 mm. Fig. 38, *Hyporosopora constricta* sp. nov., BM(NH) D55232; holotype; see also Fig. 51. Fig. 39, *Mesonopora fecunda* (Vine), BM(NH) D55155 (broken frontal wall restored); see also Fig. 60. Fig. 40, *Hyporosopora mantelli* sp. nov., USNM 69886a, holotype; see also Fig. 59. Fig. 41, *Plagioecia spissa* (Gregory), BM(NH) D5790; lectotype; see also Fig. 49. Fig. 42, *Hyporosopora larwoodi* sp. nov., BM(NH) D55099 (frontal wall broken); see also Fig. 52. Fig. 43, *Plagioecia orbifera* (Canu & Bassler), USNM 69901 (frontal wall broken and ooeciopore not visible); holotype; see also Fig. 47.

MEASUREMENTS. LAM, 0·12–0·15 mm; TAM, 0·11–0·12 mm; FWL, 0·36–0·75 mm; FWW, 0·18–0·27 mm; GW, *c.* 0·50 mm.

REMARKS. This is a common species at Faringdon and occurs on many substrates, including derived bone fragments (e.g. Fig. 36). There is no great difference between Faringdon specimens and the type specimen of *I. radiolitorum*, which is a worn specimen from the French Turonian. Possibly conspecific with *I. radiolitorum* is a second species described by d'Orbigny (1853), *Proboscina ricordeauana* from the French Aptian, represented by specimen 5694 in the d'Orbigny Colln at the MNHN. However, not only are the zooecia larger in this specimen than in the type of *I. radiolitorum*, but the type status of the specimen is dubious; it is clearly not the specimen figured by d'Orbigny.

The species is tentatively assigned to *Idmonea* on the basis of the colony growth-form, the occurrence of a marginal zone of kenozooecia and the high, rounded branches. It differs from *I. triquetra*, the Jurassic type species of *Idmonea*, notably in having rounded rather than sub-triangular branches and in the relatively short gynozooecium. Of the Cretaceous species assigned by Gregory (1899) to *Idmonea*, one (*I. hagenowi*) is a *Reptoclausa*, and the other two (*I. alipes* and *I. cristata*) have much larger marginal zones of kenozooecia than in *I. radiolitorum*.

Genus *COLLAPORA* Quenstedt, 1881

TYPE SPECIES. *Millepora straminea* (Phillips, 1829), by original designation; Bajocian of Yorkshire.

REMARKS. *Collapora* is a multisparsid with vinculariiform branches arising from an encrusting colony base.

Haplooecia Gregory, 1896 is an objective junior synomym of *Collapora* as the two genera have the same type species, *Millepora straminea* Phillips, 1829. This species has been redescribed by Illies (1968), Walter (1970) and Nye (1976). Walter (1970) incorrectly assigned the species to *Ceriocava* d'Orbigny, 1852 which is a cerioporine genus.

RANGE. Aalenian to Cenomanian.

Collapora hillmeri sp. nov. Figs 169–170 (p. 145)

HOLOTYPE. BM(NH) D58208, Little Coxwell Pit, Pitt Colln.

PARATYPES. BM(NH) D55169, Little Coxwell Pit, Thomas Colln; D55541, Little Coxwell Pit, A. G. Davis Colln; D58209–11, Little Coxwell Pit, Pitt Colln.

NAME. For G. Hillmer, West German bryozoan worker.

DESCRIPTION. Zoarium vinculariiform, arising from a small base in D58211, with dichotomizing branches about 1 mm in diameter. Growth tips have not been observed but one branch has a flattened distal end where it evidently grew against an unpreserved obstacle (Fig. 169A).

Autozooecia without clearly visible zooecial boundaries, about 12 occupying the circumference of a branch. They are variable in size, typically arranged in transverse bands of longer zooecia separated by the bands of shorter zooecia (Fig. 169B). Apertures (Fig. 169C) are of moderate diameter, subcircular or transversely elliptical in shape, with the peristome reduced to a low apertural rim. Pseudopores are circular with a density of about 2000 per mm^2.

Gynozooecia (Fig. 170A) are little inflated, longitudinally pyriform in outline, about 0·6 mm wide distally and 1·25 mm long. The ooeciopore (Fig. 170B) is located terminally and is distinctly transversely elliptical.

MEASUREMENTS. TAM, 0·08–0·12 mm; LAM, 0·05–0·08 mm; TOSM, 0·17 mm; LOSM, 0·08 mm; TOPM, 0·07 mm; LOSM, 0·03 mm.

REMARKS. This species differs from the Jurassic *Collapora straminea* in having shorter gynozooecia and a smaller, more transversely elliptical ooeciopore. The bands of alternately long and short zooecia seen in *C. hillmeri* have not been observed in *C. straminea*, but do occur in the Upper Cretaceous species *Heterohaplooecia monticulifera* Voigt & Viaud, 1983. This latter species, however, has larger autozooecia and thicker branches than *C. hillmeri*. Gynozooecia are unknown in *H. monticulifera*.

Among Faringdon bryozoans, *C. hillmeri* can be difficult to distinguish from *Entalophoroecia quadripartita* (see p. 103). The distinction between these two species was made at a late stage during the present study, following the discovery of a specimen of *C. hillmeri* with a gynozooecium. The gynozooecium is V-shaped in *E. quadripartita* but pyriform in *C. hillmeri*. *E. quadripartita* usually has numerous kenozooecia interspersed between the autozooecia, and the branches are often thinner and more straggly in appearance.

Family PLAGIOECIIDAE Canu, 1918

Genus *PLAGIOECIA* Canu, 1918

TYPE SPECIES. *Tubulipora patina* Lamarck, 1816, by original designation; Recent (see Harmelin 1976).

REMARKS. *Plagioecia* is one of several genera of superficially similar tubuloporines which were once assigned to *Berenicea* Lamouroux, a genus now regarded as a *nomen dubium* (see Taylor & Sequeiros 1982). The large, crescentic gynozooecia, pierced by autozooecia, of the type species are very distinctive. Other species commonly assigned to the genus may possess gynozooecia which are less broad but which share with the type species the presence of piercing autozooecia. The Jurassic species of *'Plagioecia'* described by Walter (1970) lack these piercing autozooecia and are more suitably placed in the genus *Hyporosopora* (see Taylor & Sequeiros 1982).

RANGE. Valanginian to Recent.

Plagioecia orbifera (Canu & Bassler, 1926) Figs 43–47

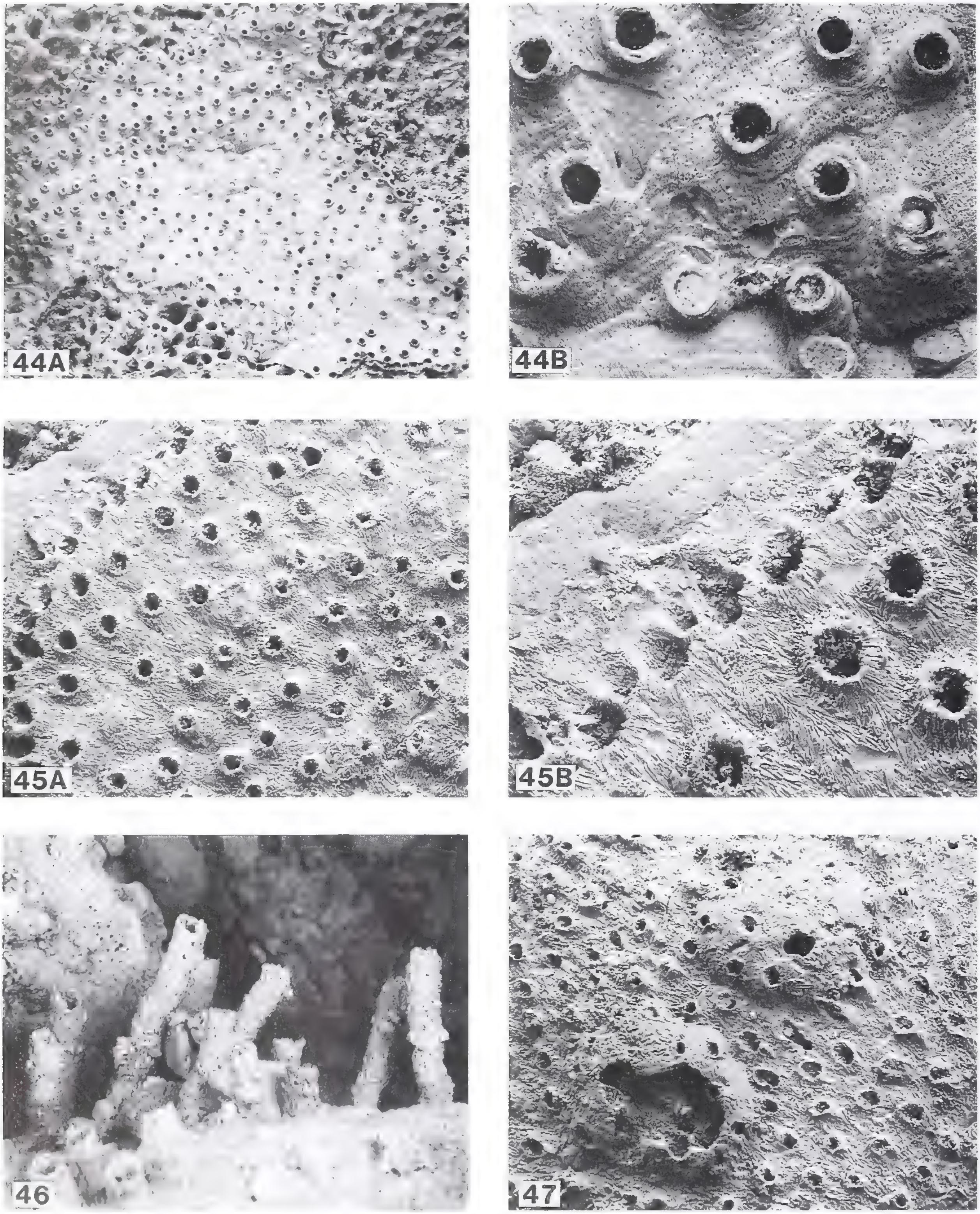
1926 *Diaperoecia orbifera* Canu & Bassler: 51; pl. 8, fig. 17
1926 *Berenicea pulchella* de Loriol; Canu & Bassler: 10 (*partim*); pl. 28, fig. 4.
1926 *Berenicea (Reptomultisparsa) tenella* de Loriol; Canu & Bassler: 12; pl. 29, figs 1–2.

HOLOTYPE. USNM 69901, figd Canu & Bassler (1926: pl. 8, fig. 17).

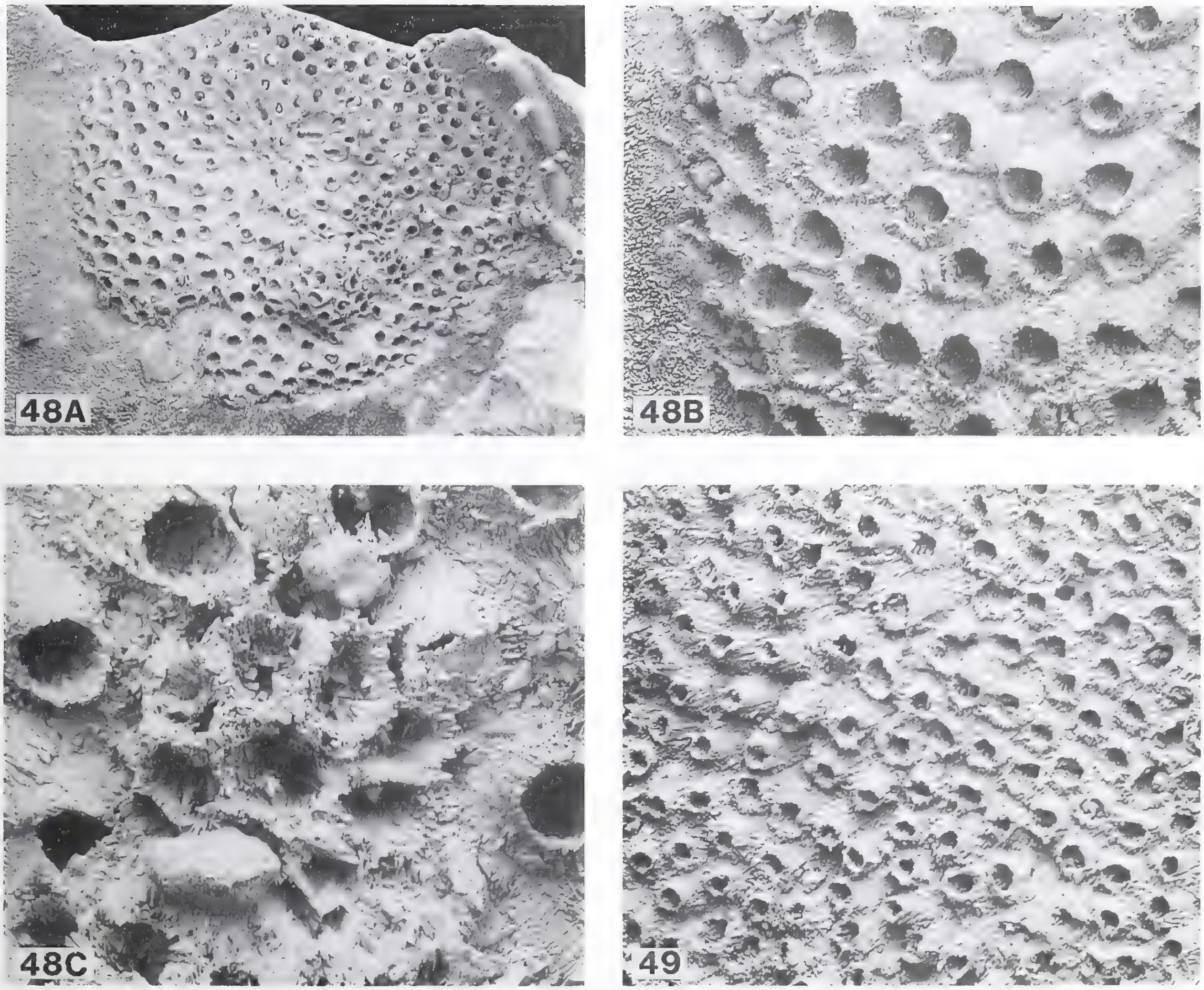
OTHER MATERIAL. BM(NH) 50781, Morris Colln; D52515, sewer trench, Little Coxwell Rd, Faringdon, Cleevely Colln; D52223, D55307 (9), Little Coxwell Pit, Pitt Colln; D55308–10, Bowler's Pit, Pitt Colln; D55311, Little Coxwell Pit, Gaster Colln: D55104, D55106 (with *'Berenicea' faringdonensis* and Stomatoporid sp. 2), Little Coxwell Pit, Thomas Colln; D55312, Little Coxwell Pit, Whiteley Colln; D55427–8, D55438–9, Wicklesham Pit, Wilson Colln.

DESCRIPTION. Zoarium adnate, bereniciform, often attaining a large size and sometimes becoming multilamellar. Growth margin thin, generally showing only one generation of zooecial buds (Fig. 45B). The discoidal form of the colony is attained rapidly with overgrowth of the ancestrula.

Autozooecia are moderately small, their frontal walls slightly convex and rather short; apertures are small, subcircular, usually surrounded by a low but distinct rim (Fig. 44B), although long peristomes (>0·7 mm) may be present in hollows on the substratum (Fig. 46). Frontal walls are crossed by irreglar transverse wrinkles in well-preserved zooecia, and have a pseudopore density of about 1300 per mm^2. Sparsely pseudoporous terminal diaphragms may be present at a level a little above that of the frontal wall.



Figs 44–47 *Plagioecia orbifera* (Canu & Bassler). Fig. 44, BM(NH) D55106; 44A, colony encrusting a sponge, × 17; 44B, autozooecia, × 90. Fig. 45, BM(NH) 50781; 45A, × 36; 45B, growth margin, × 93. Fig. 46, BM(NH) D55104, long peristomes preserved in a hollow on the substrate, × 53. Fig. 47, USNM 69901, holotype, autozooecia and two gynozooecia, × 32; see also Fig. 43.



Figs 48–49 *Plagioecia spissa* (Gregory). Fig. 48, BM(NH) D55105; 48A, small colony, × 9; 48B, growth margin showing crowded autozooecial apertures, × 37; 48C, newly-forming frontally budded subcolony, × 87. Fig. 49, BM(NH) D5790, **lectotype** (herein selected), variably spaced autozooecial apertures, × 24; see also Fig. 41.

Gynozooecia are very rare, being known only from the holotype specimen in which two poorly-preserved gynozooecia occur (Fig. 47). They are greatly inflated distally, roughly circular in outline shape, and penetrated by autozooecia (Fig. 43). The ooeciopore has not been observed; it is abraded or obscured by calcite cement overgrowth in both examples.

MEASUREMENTS. TAM, 0·06–0·08 mm; TPM, 0·09–0·12 mm; FWL, *c.* 0·60 mm; FWW, *c.* 0·18 mm; GDL, 0·88–0·91 mm; GW, 0·84–1·00 mm.

REMARKS. This is an extremely common species at Faringdon, where it is often found encrusting pebbles and sponges in association with *Hyporosopora mantelli, 'Berenicea' grandipora* and *'B.' faringdonensis*. Autozooecial dimensions are considerably smaller than in the latter two of these, and a little larger than in *H. mantelli*, and the autozooecia have a distinct apertural rim absent in *H. mantelli*.

The fact that the gynozooecium is pierced by autozooecia suggests assignment to *Plagioecia*, although the distal dilated part is almost equidimensional whereas most species of *Plagioecia* have transversely elongate gynozooecia.

Berenicea pulchella de Loriol, 1863 and *B. tenella* de Loriol, 1868 are difficult to interpret from the original descriptions or from material in the MHNG. However, it is doubtful if either of these Swiss Valanginian species is the same as *P. orbifera* from Faringdon. Walter's (1972) redescription of *B. pulchella*, which he refers to *Plagioecia*, notes the heart-shaped gynozooecium, which is unlike that of *P. orbifera*. According to Walter (1972), *B. tenella*, also reassigned to *Plagioecia*, has a colony formed of subcircular subcolonies. Such structures are not present in *P. orbifera*.

Plagioecia spissa (Gregory, 1899) Figs 41, 48–49

1899 *Berenicea spissa* Gregory: 108; pl. 7, fig. 4.
1926 *Cellulipora spissa* (Gregory) Canu & Bassler: 6; pl. 26, figs 8–9.
1967 *'Cellulipora' spissa* (Gregory); Walter: 58; pl. 12, figs 5–6.
1972 *Cellulipora spissa* (Gregory); Buge & Voigt: 140.
?1984 *Cellulipora spissa* (Gregory); Delamette & Walter: 33; pl. 5, figs 1–2.

LECTOTYPE. BM(NH) B5790 (figd Gregory 1899: pl. 7, fig. 4), old collection, selected herein as the lectotype.

PARALECTOTYPES. BM(NH) D3024, Caleb Evans Colln; D3029, old collection.

OTHER MATERIAL. BM(NH) D55105, Little Coxwell Pit, Pitt Colln; D55314 (5), locality presumed to be Faringdon, *ex* Durham University Colln; D55315, D55316 (4), Little Coxwell Pit, Whiteley Colln; D55317 (3), Little Coxwell Pit, Cleevely Colln.

DESCRIPTION. Zoarium a discoidal sheet (bereniciform), often relatively large (diameter sometimes 20 mm). Growing edge usually revealing only one generation of zooecial buds (Fig. 48B); distal fringe of basal lamina wide, extending up to 0·5 mm away from the budding zone. Ancestrula and early zooecia apparently overgrown by lateral lobes of the initially fan-shaped zoarium. Multilamellar zoaria are occasionally produced by the frontal budding of discoidal subcolonies (Fig. 48C).

Autozooecia in primary zone of astogenetic change are slender with longitudinally elongate apertures; those in the zone of astogenetic repetition are short with subcircular or transversely elongate apertures (Fig. 48B) which are crowded, variable in size and lack peristomes. Areas of autozooecia with long frontal walls and widely-spaced apertures may be developed (Fig. 49), forming maculae (cf. the branching erect tubuloporine *Heterohaplooecia* Voigt & Viaud, 1983).

Gynozooecia are diffuse, longitudinally ovoidal, and penetrated by numerous autozooecia (Fig. 41); the ooeciopore is transversely elongate, smaller than an autozooecial aperture and positioned well proximally.

MEASUREMENTS (made from the lectotype). LAM, 0·09–0·18 mm; TAM, 0·12–0·15 mm; FWL, 0·36–0·57 mm; FWW, 0·21–0·30 mm; GDL, *c*. 1·4 mm; GW, *c*. 1·3 mm.

REMARKS. The lectotype specimen consists of two colonies of similar size which originate on the interior surface of the pedicle valve of a brachiopod, apparently fuse with one another, and extend onto the exterior surface of the brachiopod. Gregory's figure (1899: pl. 7, fig. 4) depicts a worn area of colony on the exterior of the brachiopod.

This is a common species at Faringdon which is distinctive by virtue of the closely-spaced apertures in zones of astogenetic repetition. Although apparently unknown elsewhere in the British Cretaceous, Canu & Bassler (1926) recorded *P. spissa* from the Aptian of d'Ervy, Switzerland, and Buge & Voigt (1972) from the Hauterivian of Hauteville, France. Assignment to the genus *Cellulipora*, as suggested by Canu & Bassler (1926), is doubtful because the Faringdon species lacks the well-defined, regularly-arranged, polygonal subcolonies bounded by zones of kenozooecia which are present in the type species, *C. ornata* from the Cenomanian of Le Havre, France (see Buge & Voigt 1972). The gynozooecium suggests placement in *Plagioecia*.

Genus ***HYPOROSOPORA*** Canu & Bassler, 1929

TYPE SPECIES. *Hyporosopora typica* Canu & Bassler, 1929, by original designation; Bathonian of France.

REMARKS. This genus of bereniciform tubuloporines is distinguished by the form of the gynozooecium which is moderately broad and varies in outline from subtriangular (as in the type species) to boomerang-shaped with lateral lobes extending distally of the level of the ooeciopore (see Taylor & Sequeiros 1982). Autozooecia do not penetrate the gynozooecium (as they do in *Plagioecia*), and the margins of the gynozooecium are not diffuse with deep embayments formed by autozooecia (as in *Mesonopora*).

RANGE. Aalenian to ?Recent.

Hyporosopora constricta sp. nov. Figs 38, 50–51

HOLOTYPE. BM(NH) D55232, Little Coxwell Pit, Pitt Colln.

PARATYPES. BM(NH) D55097, Little Coxwell Pit, Pitt Colln; D55230, Little Coxwell Pit, Gaster Colln; D55231, Little Coxwell Pit, Thomas Colln.

NAME. 'Constricted', referring to the autozooecial apertures.

DESCRIPTION. Zoaria are thin, discoidal (bereniciform), typically small, sometimes lobate, with a narrow distal fringe of basal lamina and one tier of zooecia visible at the growing edge (Fig. 51B). The ancestrula is overgrown by latter zooecia.

Autozooecia are slender, with peristomes well raised (up to 0·3 mm high; Fig. 51A), apertures longitudinally elliptical and constricted medially by groups of blunt mural spines growing inwards from the sides of the aperture at about the height of the colony surface (Fig. 50B). Frontal walls are transversely wrinkled with sparse teardrop-shaped pseudopores pointed distally, about 800–1000 per mm^2. Occluded autozooecia are occasionally present, their terminal diaphragms level with the colony surface and bearing sporadic, irregularly-shaped pseudopores (Fig. 50C).

Gynozooecia are subtriangular, and deeply indented by the surrounding autozooecia (Figs 38, 51C); the ooeciostome is strongly reflexed proximally, the ooeciopore considerably smaller than an autozooecial aperture.

MEASUREMENTS. LAM, mean 0·12 mm; TAM, mean 0·06 mm; LPM, mean 0·14 mm; TPM, mean 0·10 mm; FWL, 0·60–0·70 mm; FWW, 0·13–0·15 mm; GDL, 0·50–0·60 mm; GW, 0·70–0·90 mm; LOPM, 0·05–0·06 mm; TOPM, 0·06–0·08 mm; LOSM, 0·08 mm; TOSM, 0·09–0·11 mm.

REMARKS. This species is distinguished from previously described bereniciform tubuliporines by the presence of groups of mural spines (intrazooecial spines) forming a medial constriction to the autozooecial aperture. Although these structures are clearly visible in the well-preserved type material, they may not be recognizable in specimens of inferior preservation.

Available specimens encrust brachiopods and sponges.

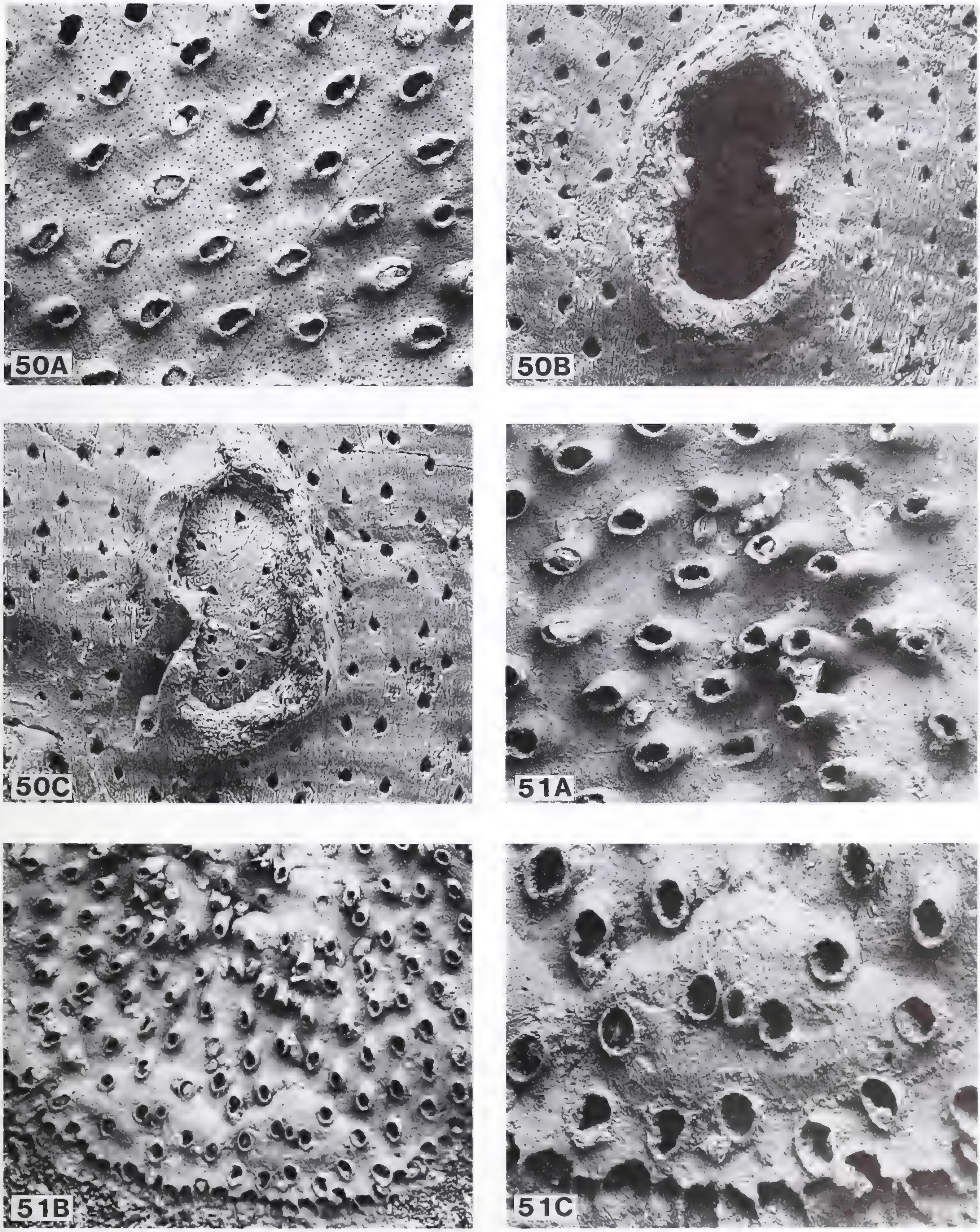
Hyporosopora larwoodi sp. nov. Figs 42, 52–56

HOLOTYPE. BM(NH) D55096, *ex* Durham University Colln.

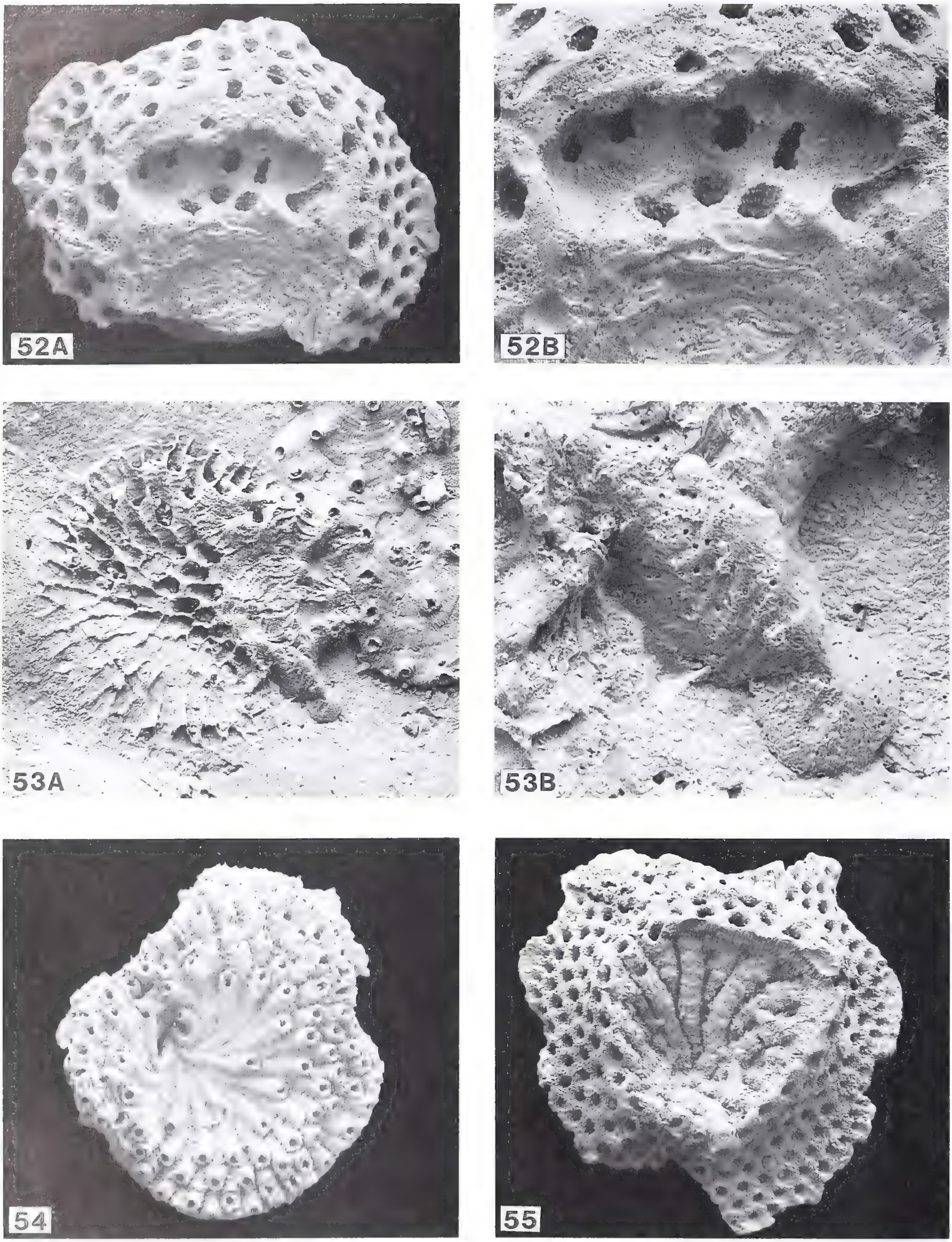
PARATYPES. BM(NH) D55097–8, D57938, Little Coxwell Pit, Elliott Colln; D55221–4, Little Coxwell Pit, Thomas Colln; D55227, Little Coxwell Pit, Pitt Colln; D55228, Little Coxwell Pit, Whiteley Colln; D55229, Bowler's Pit, Gaster Colln; D57597, Little Coxwell Pit, Pitt Colln. USNM 69000 (with the holotype of *Oncousoecia coarctata* (Canu & Bassler))

NAME. In recognition of the scientific contributions of bryozoologist Dr Gilbert P. Larwood (University of Durham).

DESCRIPTION. Zoaria adnate, small (usually less than 3 mm in diameter), and bereniciform, circular (Fig. 55) or fan-shaped



Figs 50–51 *Hyporosopora constricta* sp. nov. Fig. 50, BM(NH) D55097; 50A, autozooecia, × 38; 50B, autozooecial aperture constricted by groups of mural spines, × 270; 50C, autozooecial aperture with terminal diaphragm, × 255. Fig. 51, BM(NH) D55232, **holotype**: 51A, autozooecia with long peristomes, × 41; 51B, × 23; 51C, gynozooecium and ooeciopore (distal direction is downwards), × 54; see also Fig. 38



Figs 52–55 *Hyporosopora larwoodi* sp. nov. Fig. 52, BM(NH) D55099; 52A, broken, free colony, × 36; 52B, fractured gynozooecium, × 69; see also Fig. 42. Fig. 53, USNM 69000, colony encrusting the same substrate as the holotype of *Oncousoecia coarctata* (Canu & Bassler); 53A, abraded fan-shaped colony overgrowing *O. coarctata*, × 30; 53B, ancestrula, × 115. Fig. 54, BM(NH) D55098, free colony with concentration of autozooecial apertures close to the growth margin, × 26. Fig. 55, BM(NH) D57938, small, free colony with thick growth margin, × 38.

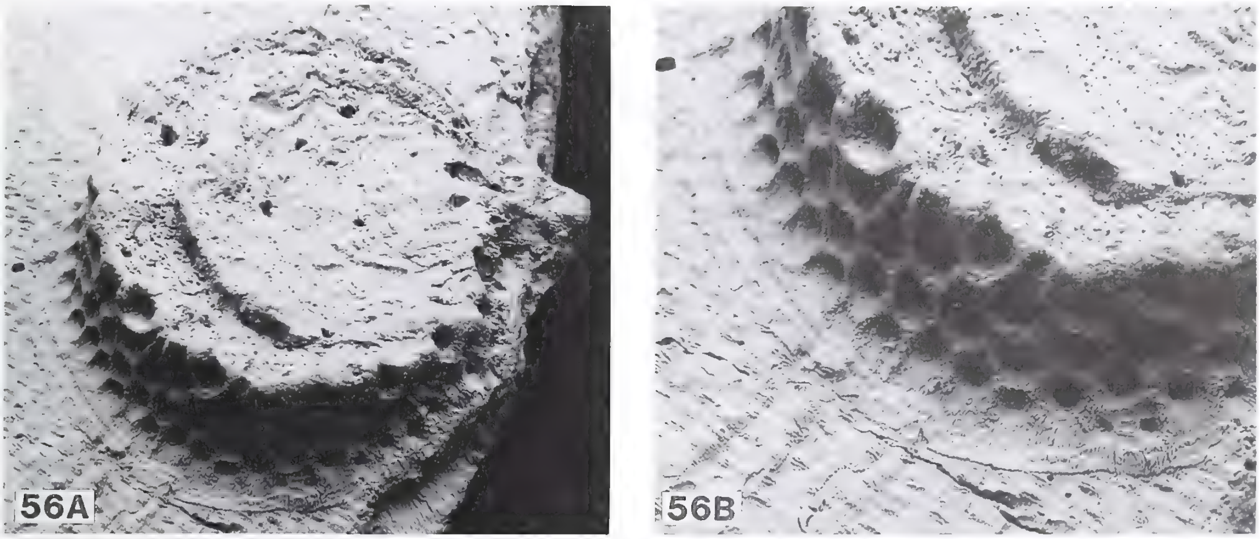


Fig. 56 *Hyporosopora larwoodi* sp. nov., BM(NH) D55096, **holotype**; 56A, oblique view showing thick growth margin and absence of apertures on the frontal surface of the colony, × 29; 56B, growth margin, × 60.

(Fig. 53A) in outline. Fan-shaped peripheral subcolonies may be developed from the main colony. In some colonies (Figs 55, 56), zooecia open only at the thick colony growing edge which reveals several tiers of zooecia. The pseudoporous frontal surface of the colony is devoid of apertures in these colonies and may be rugose with closely-spaced transverse wrinkles (Fig. 56A), with or without longitudinal ridges (Fig. 55) corresponding to the frontal walls of individual zooecia. In other colonies, zooecial apertures are present on the frontal surface, typically sparsely distributed in the depressed proximal part of the colony but closely spaced near the edge of the colony (Fig. 54). The distal fringe of the basal lamina extends up to 0·1 mm away from the budding zone.

Autozooecia opening on frontal surfaces of colonies intersect the surface at an acute angle and have circular or transversely elongate apertures with thick rims. Blade-like mural spines have been observed within fractured autozooecia.

The ancestrula has a protoecium about 0·21 mm in diameter (Fig. 53B).

Gynozooecia (Figs 42, 52) have transversely elliptical frontal walls (broken in all available specimens) and terminal, transversely elongate ooeciopores smaller than the autozooecial apertures.

Measurements. TAM, *c.* 0·11 mm; FWW, *c.* 0·18 mm; GDL, 0·40 mm; GW, 1·00 mm; TOPM, 0·08 mm; LOPM, 0·05 mm.

Remarks. This species is characterized by the small but thick colonies whose frontal surfaces either lack apertures or have apertures concentrated in a band close to the periphery of the colony. The zooecia make a shallow angle with the colony surface and it seems likely that slight variations in this angle determine whether zooecia open on the frontal surface of the colony or only at the thick growing edge of the colony. The latter condition gives a morphology resembling the Palaeozoic genus *Flabellotrypa* (see Brood 1975). Zooecial frontal wall length is extremely variable; the shortest zooecia are only 0·20 mm long, whereas incomplete zooecia (whose distal parts are still at the growing edge) may exceed 1·4 mm in length. No previously described species from the Cretaceous has this characteristic colony morphology.

H. larwoodi is relatively common in the Faringdon Sponge Gravel and can be found as small colonies encrusting a wide variety of substrates, or in sediment samples as detached colonies (Figs 52, 54–55) which apparently grew on perishable substrates.

Hyporosopora mantelli sp. nov. Figs 40, 57–59

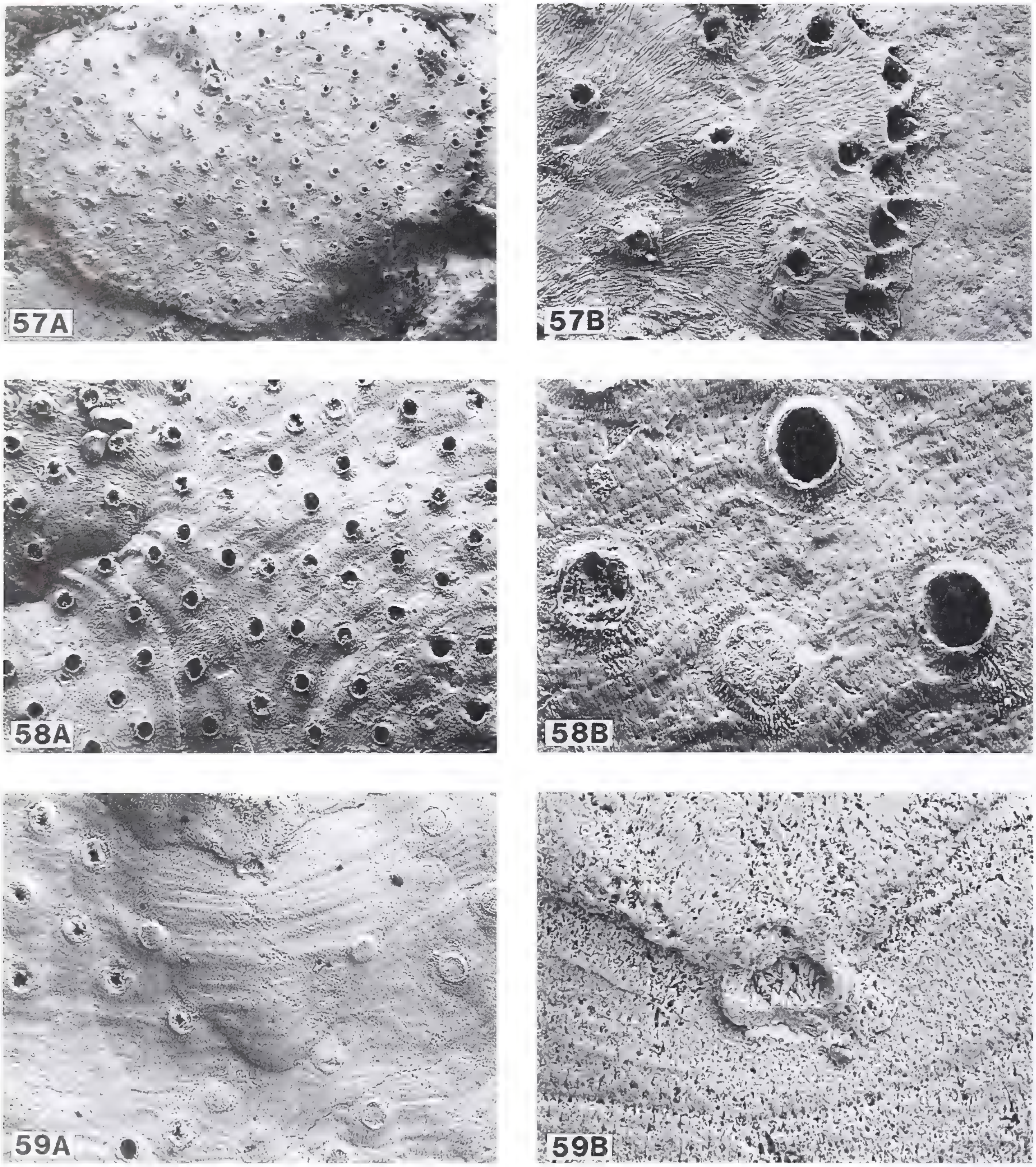
1883 ?*Reptomultisparsa haimeana* de Loriol; Keeping: 137.
1899 *Reptomultisparsa haimei* (de Loriol); Gregory: 117; fig. 5.
1926 *Trigonoecia haimei* (de Loriol); Canu & Bassler: 39 (*partim*); pl. 1, figs 10–12 only.

Holotype. USNM 69886a, figd by Canu & Bassler (1926: pl. 1, fig. 12).

Paratypes. BM(NH) 10265 (figd by Gregory 1899: fig. 5), Mantell Colln; 50781, Morris Colln; D55072, D55127, D55129, D55131, Little Coxwell Pit, Gaster Colln; D55073, Little Coxwell Pit, Whiteley Colln; D55128, Gaster Colln; D55130, Little Coxwell Pit, Pitt Colln; D55428, Wicklesham Pit, Wilson Colln. SM B27889–91, encrusting a piece of bone and labelled '*Diastopora oceanica*'; B27959, labelled '*Ceriopora polymorpha*'. USNM 69886b (figd by Canu & Bassler 1926, pl. 1: fig. 10 as *Trigonoecia haimei*).

Name. For Gideon Mantell, the famous 19th Century fossil collector who collected one of the paratypes.

Description. Zoarium adnate, initially unilamellar (Fig. 57A) and subcircular (bereniciform), becoming multilamellar by the addition of subcolonies which begin as subcircular overgrowths, apparently produced by eruptive frontal budding. Multilamellar colonies may attain a considerable size: specimen BM(NH) 10265 has ten or more layers and covers most of a cup-shaped sponge 8 cm in diameter. Zoarial layers are very thin (*c.* 0·25 mm) and only one tier of buds is



Figs 57–59 *Hyporosopora mantelli* sp. nov. Fig. 57, BM(NH) 50781; 57A, × 17; 57B, growth margin with single tier of zooecial buds, × 65. Fig. 58, BM(NH) D55072; 58A, × 32; 58B, autozooecial apertures, one with a terminal diaphragm, × 141. Fig. 59, USNM 69886a, **holotype**; 59A, gynozooecium, × 46; 59B, ooeciopore, × 200; see also Fig. 40.

normally visible at the growing edge (Fig. 57B). The distal fringe of the basal lamina is not extensive. Zoarial surfaces are flat but may be crossed by irregular transverse wrinkles of low amplitude (Fig. 58A). Colonies have a characteristically shiny appearance when viewed with an optical microscope.

Autozooecia are immersed, small, slender, and have rounded, slightly dilated distal ends. Apertures are very small, circular or longitudinally elongate, widely spaced, and lack significant peristomes (Fig. 58B). Sparsely pseudoporous terminal diaphragms may occur. Pseudopores are subcircular and occur at a density of about 2000 per mm^2. The ancestrula is overgrown by later zooecia.

Gynozooecia are rare, their distal frontal walls are of low profile, subtriangular in outline (Figs 40, 59A), a little wider than long, with lateral lobes extending a little distal of the ooeciopore. The ooeciopore is transversely elongate (Fig. 59B).

MEASUREMENTS (determined from 10 autozooecia and 1 gynozooecium in the holotype). LAM, 0·08–0·09 mm; TAM, 0·06–0·09 mm; FWL, 0·45–0·72 mm; FWW, 0·15–0·21 mm; GTL, 1·32 mm; GDL, 0·93 mm; GW, 1·22 mm; LOPM, 0·05 mm; TOPM, 0·08 mm.

REMARKS. This new species was first described from Faringdon as *Reptomultisparsa haimei* de Loriol by Gregory (1899), who gave no reason for changing the species name from de Loriol's *haimeana* to *haimei*. The figured type specimen of *R. haimeana* (MHNG 29635, from the Neocomian of Salève) has been examined and found to differ from the Faringdon species in the considerably larger size of the zooecia (TAM = 0·12 mm, cf. 0·04–0·06 mm). A second de Loriol species, *Berenicea pulchella* (figured type MHNG 29625, which is poorly preserved and has slightly smaller zooecia), may be a synonym of *R. haimeana* de Loriol.

Canu & Bassler (1926) described supposed *Trigonoecia haimeana* (de Loriol) from both Switzerland (Ste Croix) and Faringdon. Their Ste Croix material (including USNM 69885, depicted in their pl. 1, fig. 9) has more prominent zooecia with a closer spacing of the apertures than the Faringdon specimens and is regarded as a different species.

Gregory (1899) incorrectly gave the apertural diameter of *H. mantelli* as 0·10 mm, and erroneously described the zoarial layers as thick, possibly because he studied a worn part of the solitary specimen (BM(NH) 10265) which was available to him.

H. mantelli is commonly found encrusting sponges but can also be found on other substrates, especially pebbles.

Genus ***MESONOPORA*** Canu & Bassler, 1929

TYPE SPECIES. *Mesonopora typica* Canu & Bassler, 1929 (= *Berenicea concatenata* Reuss, 1867, *fide* Walter, 1970: 132); Middle Jurassic, Poland.

REMARKS. *Mesonopora* is a genus of bereniciform plagioeciids in which the gynozooecium is strongly indented at its margins by autozooecia but, unlike *Plagioecia*, is not pierced by autozooecia (see Taylor & Sequieros 1982).

RANGE. Bathonian to ?Recent.

Mesonopora fecunda (Vine, 1885) Figs 39, 60–61

?1868 *Reptomultisparsa tenella* de Loriol: 61; pl. 5, figs 15–16.
1885 *Diastopora fecunda* Vine: 18.
1889 *Diastopora fecunda* Vine; Vine: 266.
?1891 *Diastopora fecunda* Vine; Vine: 379.
1899 *Reptomultisparsa congesta* (Reuss); Gregory: 118 (*partim*); pl. 6, fig. 5 only.
1989 *Mesonopora tenella* (de Loriol); Walter: 134; text-fig. 15; pl. 7, figs 2–5; pl. 8, figs 1–6; pl. 9, figs 5–9.

MATERIAL. BM(NH) D55090–1, Little Coxwell Pit, Whiteley Colln; D55155 (several colonies encrusting a sponge), Treacher Colln (*ex* University of Reading Collection); D55156, Little Coxwell Pit, Pitt Colln.

DESCRIPTION. Zoarium encrusting, discoidal bereniciform (Fig. 60B, C), thick (*c.* 0·8 mm), with a deep growth margin showing 3 to 8 tiers of zooecial buds (Fig. 60D). In one specimen the growth margin is raised free of the substrate. Discoidal peripheral subcolonies (Fig. 60A), up to 4 mm in diameter, arise at the growing edge and overlap parent subcolonies, giving a compound colony of offset discs. The ancestrula is overgrown by later zooecia.

Autozooecia are slender, moderately large, with distally convex, poorly-defined frontal walls and small, closely-spaced, longitudinally elliptical apertures without significant peristomes. Terminal diaphragms, which may occlude the ontogenetically older zooecia, are sparsely pseudoporous and are situated at or slightly above frontal wall level. In good preservation the frontal walls are seen to be crossed by irregular, sinous, transverse ridges (Fig. 61A). Pseudopores are usually present only between the ridges, in a density of approximately 1300 per mm^2. Tubercle-like mural spines are visible in some zooecial buds (Fig. 61B).

Gynozooecia (Figs 39, 60B) are large, very broad and crescent-shaped, their margins indented by autozooecia. The ooeciopore cannot be identified with certainty in the abraded material available.

MEASUREMENTS. TAM, 0·04–0·06 mm; FWW, 0·07–0·10 mm; GDL, *c.* 1·00 mm; GW, *c.* 4·00 mm.

REMARKS. The type specimen of *Mesonopora fecunda* Vine is BM(NH) B4452 from the Cambridge Greensand (Cenomanian). Apparently conspecific specimens from Faringdon share the discoidal offset subcolonies of the type and have similar zooecial dimensions. However, determination of the Faringdon material as *Mesonopora fecunda* must remain provisional until larger suites of better-preserved specimens from Faringdon and Cambridge become available.

It is possible that the Faringdon species is the same as *Reptomultisparsa tenella* de Loriol, but the type material of this species is missing from the collections of the MHNG.

Although this species is here assigned to *Mesonopora*, the occurrence of marginal discoidal subcolonies invites comparison with *Plagioecia patina* (Lamarck), the Recent type species of *Plagioecia* (see Hayward & Ryland 1985).

This is a rare species at Faringdon. Of the poorly-preserved colonies in the BM(NH) collections, three encrust sponges and one a branch fragment of *Meliceritites gracilis*.

Genus ***UNITUBIGERA*** d'Orbigny, 1853

TYPE SPECIES. *Unitubigera discus* d'Orbigny, 1853, by subsequent designation of Bassler, 1935; Neocomian of Ste Croix.

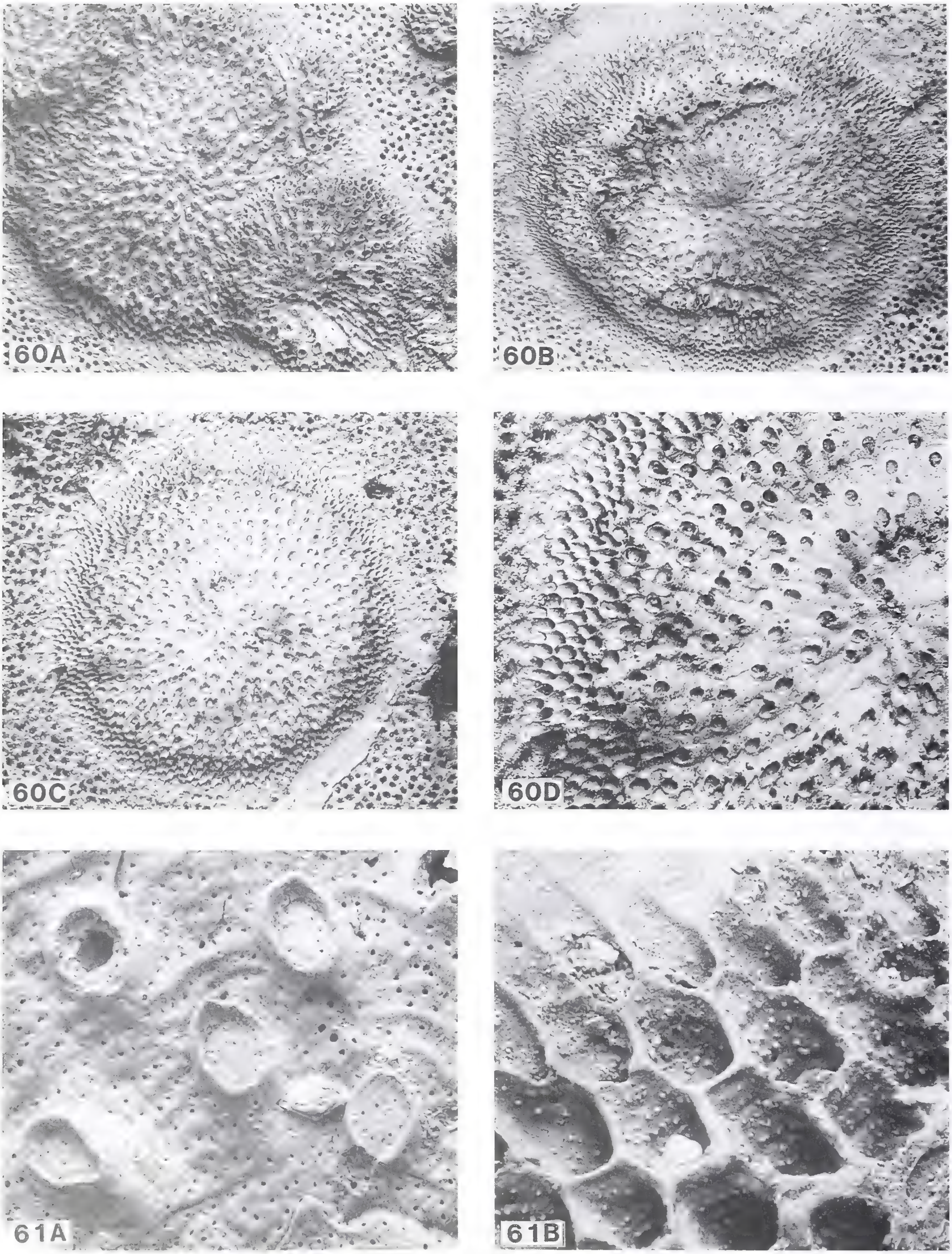
REMARKS. Bereniciform tubuloporines with apertures arranged uniserially in connate, radial rows are placed in the genus *Unitubigera*. Walter (1987*b*) has redescribed the type species and provided a revised diagnosis for *Unitubigera*.

RANGE. Uncertain, possibly Valanginian to Miocene.

Unitubigera sp. Fig. 62

MATERIAL. BM(NH) D55112, Little Coxwell Pit, Gaster Colln; D55116, Little Coxwell Pit, Pitt Colln.

DESCRIPTION. Zoarium encrusting (Fig. 62A), discoidal, approximately circular in outline, 6–8 mm in diameter. Several generations of zooecial buds are visible at the growing edge.



Figs 60–61 *Mesonopora fecunda* (Vine). Fig. 60, BM(NH) D55155, several colonies encrusting a sponge. 60A, colony with peripheral subcolony, × 10; 60B, colony with abraded gynozooecia, × 12; 60C, discoidal colony showing thick growth margin, × 10; 60D, detail of the colony shown in 60C, × 23; see also Fig. 39. Fig. 61, BM(NH) D55090; 61A, autozooecia with terminal diaphragms and transversely ridged frontal walls, × 171; 61B, zooecial buds with tubercle-like mural spines, × 171.

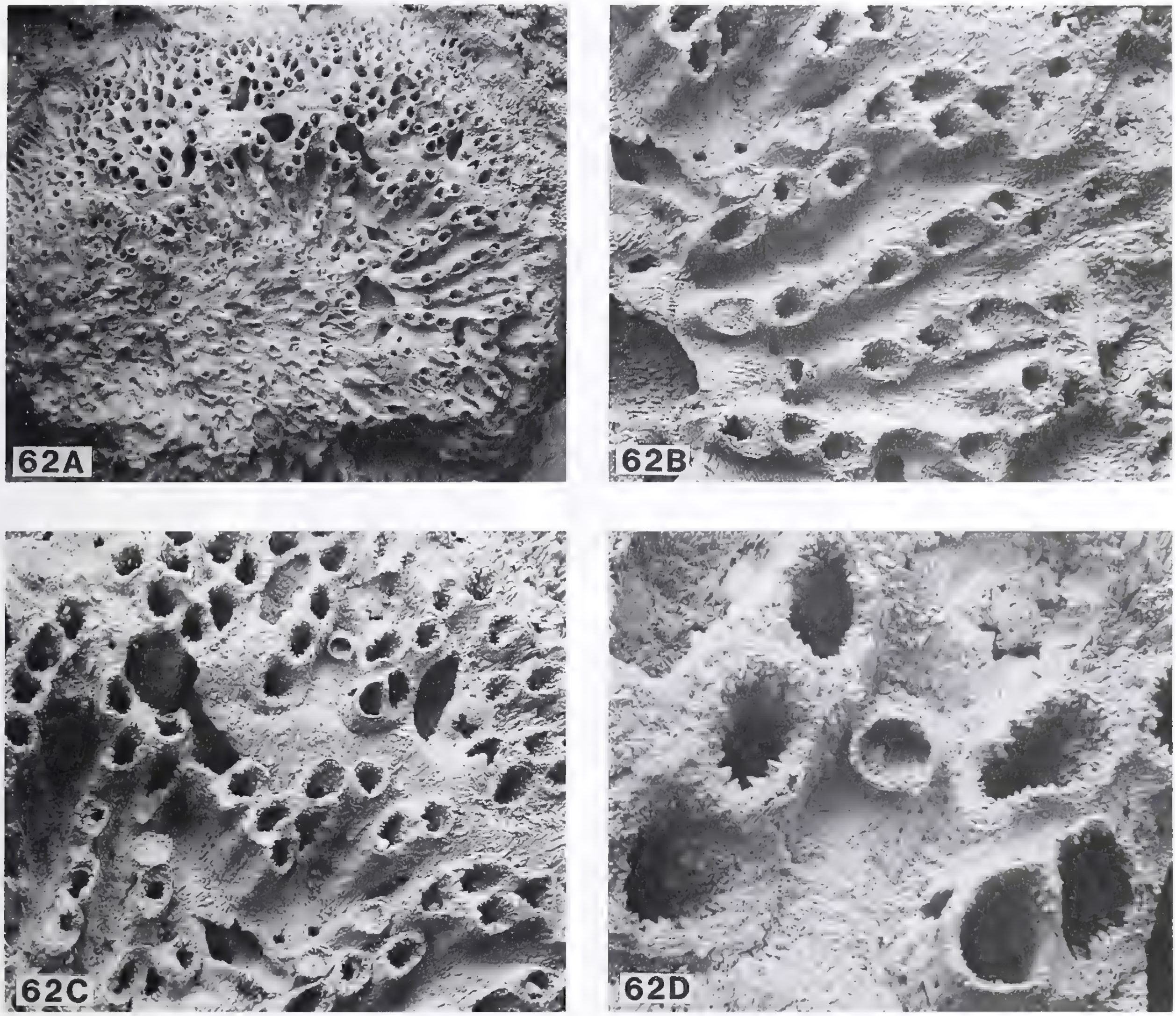


Fig. 62 *Unitubigera* sp., BM(NH) D55116; 62A, partly overgrown colony, × 11; 62B, radial rows of autozooecial apertures, × 41; 62C, broken gynozooecium, × 33; 62D, ooeciopore, × 116.

Autozooecial apertures are longitudinally elongate and arranged uniserially in radial rows with successive apertures barely connate (Fig. 62B). Peristomes are inclined at a low angle to the colony surface.

Gynozooecia (Fig. 62C) have distal frontal walls which are diffuse, transversely elongate and indented at their edges by autozooecial apertures. Ooeciopores (Fig. 62D) are located between rows of autozooecia and are transversely elongate, the ooeciostome being reflexed proximally.

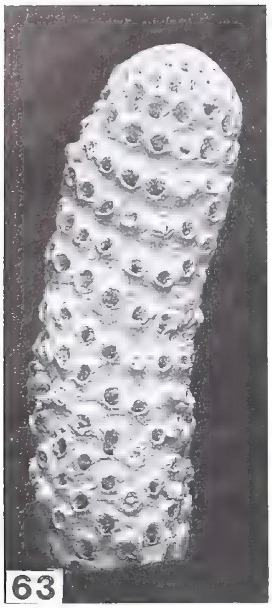
MEASUREMENTS. TAM, 0·07–0·10 mm; TPM, 0·10–0·17 mm; FWW, 0·15–0·17 mm; GDL, 0·40–0·70 mm; GW, 0·60–2·00 mm; LOPM, 0·05–0·07 mm; TOPM, 0·09–0·10 mm.

REMARKS. This is a rare species in the Faringdon Sponge Gravel. Both of the available specimens encrust sponges and both have gynozooecia. Their preservation, however, is poor. They may belong to the species *Unitubigera discus* d'Orbigny 1853, originally described from the Valanginian of Ste Croix and later revised by Walter (1972, 1987*b*). However, a probable specimen of *U. discus* from the Lower Tealby Clay (Hauterivian) of Nettleton (BM(NH) D52791) has significantly larger autozooecial apertures than the material from Faringdon.

Unitubigera and the similar genus *Actinopora* have been recorded in error from Faringdon on at least two occasions. A specimen in the Davey Collection (OUM K 53) labelled *Unitubigera papyracea* is presumably the specimen Davey records in his species lists (1877: 7 and 1905: 28). This specimen is actually a worn *Idmonea radiolitorum* partially covered by a colony of *Reptomultisparsa*. Specimens labelled as *Actinopora* in the BGS Collections (Tablet D 32/2, specimens 43761 and 43762) are *Reptoclausa hagenowi*, as pointed out by Gregory (1909*b*: 239). These could well be the specimens recorded by Sharpe (1854: 189) as *Actinopora*. True *Actinopora*, distinguished from *Unitubigera* by the multiserial (often biserial) arrangement of the connate zooecial apertures, appears to be absent from Faringdon.

Genus ***CARDIOECIA*** Canu & Bassler, 1922

TYPE SPECIES. *Bidiastopora neocomiensis* d'Orbigny, 1853, by original designation; Neocomian of Ste Croix, Switzerland.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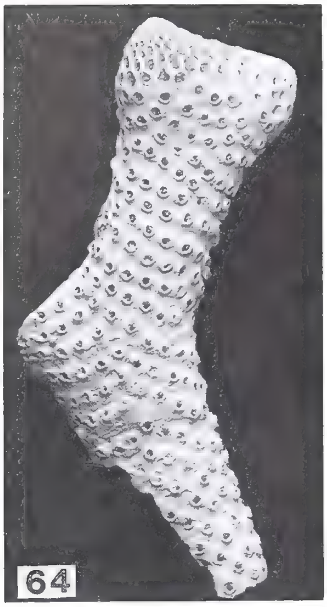
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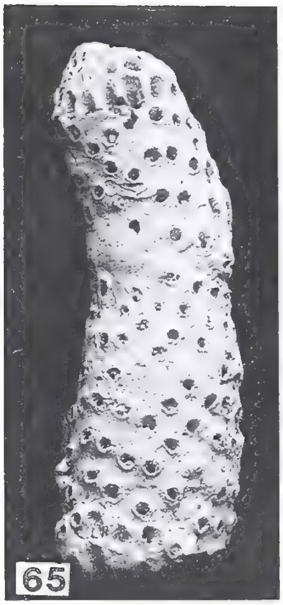
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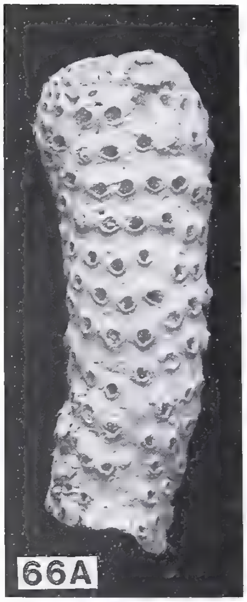
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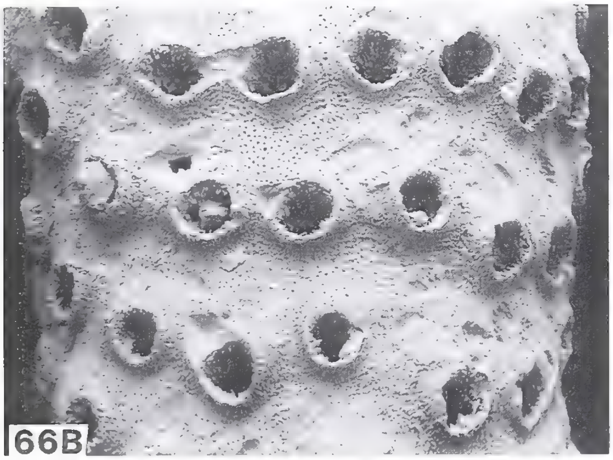
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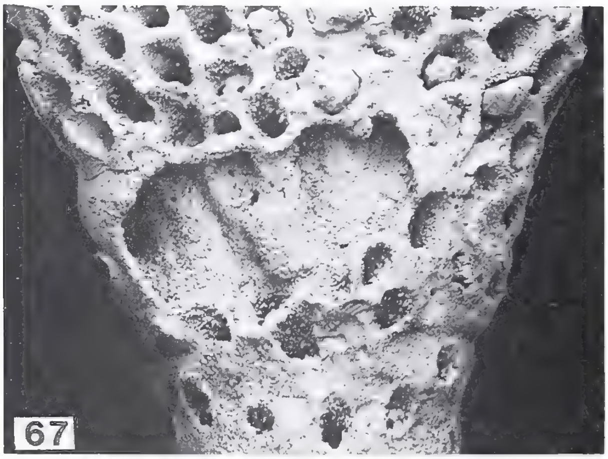
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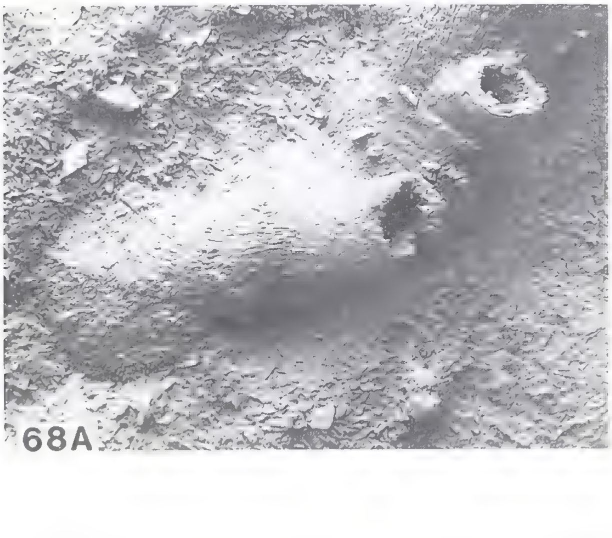
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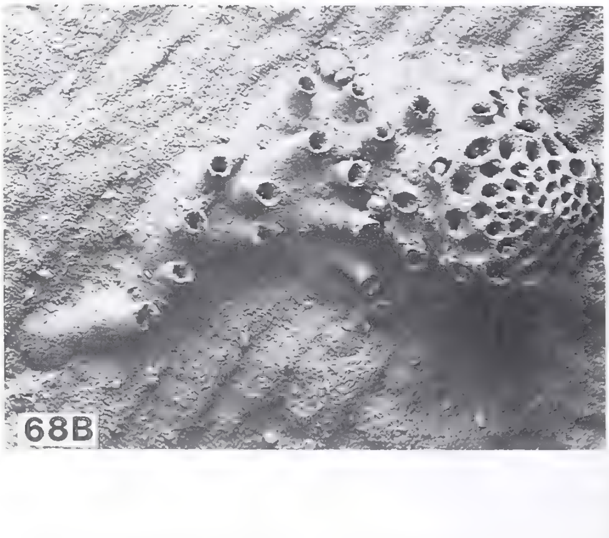

68B

Figs 63–68 *Cardioecia neocomiensis* (d'Orbigny). Fig. 63, USNM 69893e, × 13. Fig. 64, USNM 69893d, × 10. Fig. 65, USNM 69898, holotype of *C. pauper* Canu & Bassler, × 12. Fig. 66, BM(NH) D55081; 66A, × 10; 66B, autozooecia, × 41. Fig. 67, BM(NH) D55074, broken gynozooecium, × 23. Fig. 68, BM(NH) D53698; 68A, ancestrula, × 47; 68B, colony base with short erect stem, × 15.

REMARKS. *Cardioecia* is a plagioeciid characterized by erect vinculariiform branches which have a short median budding lamina. Possible extant species of the genus are known (Harmelin 1976), but at least some of them lack the probosciniform bases present in the type species.

As the type species of *Notoplagioecia* Canu & Bassler, 1922 (*N. farringdonensis* Canu & Bassler, 1922) is considered to be a junior synonym of the type species of *Cardioecia*, the genus *Notoplagioecia* is here placed in synonymy with *Cardioecia*.

RANGE. Valanginian to ?Recent.

Cardioecia neocomiensis (d'Orbigny, 1853) Figs 63–69

1853 *Bidiastopora neocomiensis* d'Orbigny: 800; pl. 784, figs 9–11.
1922 *Cardioecia (Bidiastopora) neocomiensis* (d'Orbigny) Canu & Bassler: 19; pl. 4, fig. 3.
1922 *Notoplagioecia farringdonensis* Canu & Bassler: 30; pl. 1, fig. 18.
?non 1926 *Cardioecia neocomiensis* (d'Orbigny); Canu & Bassler: 40; pl. 2, figs 1–7; fig. 19A–B.
non 1926 *Cardioecia neocomiensis parvula* Canu & Bassler: 42; pl. 2, fig. 8.
?1926 *Cardioecia neocomiensis entalophoroides* Canu & Bassler: 42; pl. 2, figs 9–10.
1926 *Cardioecia faringdonensis* Canu & Bassler: 44; pl. 3, figs 9–15; fig. 19E–G.
1926 *Cardioecia pauper* Canu & Bassler: 44; pl. 5, figs 1–2.
1926 *Notoplagioecia faringdonensis* [sic] Canu & Bassler: 48; pl. 5, figs 3–5; fig. 22.
?1965 *Cardioecia neocomiensis* (d'Orbigny); Cotillon & Walter: 934; pl. 40, fig. 7.
1966 *Mesenteripora neocomiensis* (d'Orbigny) Walter: 898; pl. 26, figs 9–10.
?1966 *Mesenteripora campicheana* (d'Orbigny); Walter: 898; pl. 26, figs 11–12.
1967 *Mesenteripora sanctacrucensis* nom. nov., Walter: 56.
1971 *Cardioecia neocomiensis* (d'Orbigny); Hillmer: 55; pl. 6, figs 1–5; text-figs 14–15.
1971 *'Cardioecia' faringdonensis* Canu & Bassler; Hillmer: 58; pl. 6, figs 7–11; text-fig. 16.
1972 *Mesenteripora sanctacrucensis* Walter; Walter: 313 [?*partim*]; pl. 21, figs 8–9.
1975 *Entalophora faringdonensis* (Canu & Bassler); Walter *et al.*: 99; pl. 8, figs 8–10.
1985 *Mesenteripora sanctacrucensis* Walter; Walter: 16; pl. 5, figs 1–7, pl. 6, figs 3–7 (non figs 1–2); pl. 9, fig. 12 (non figs 13–15).

MATERIAL. BM(NH) D7465 (colony base encrusting a pebble), Cunnington Colln; D7980 (colony base encrusting a pebble), Treacher Colln; D38853, D52196 (7 colony bases), D55074 (3), D55075 (2), D55076, D55077 (2), D55078–81, D55136, Little Coxwell Pit, Pitt Colln; D53698 (colony base), D57645, Little Coxwell Pit, Davis Colln; D55132, Bowler's Pit, Pitt Colln; D55133 (2), Bowler's Pit, Gaster Colln; D55134 (4), Little Coxwell Pit, Gaster Colln; D55135 (sample), D55137 (3), Little Coxwell Pit, Thomas Colln; D55138 (sample), Cleevely Colln. USNM 69893 (5 + thin sections), syntypes of *Cardioecia faringdonensis* Canu & Bassler; 69898, holotype of *Cardioecia pauper* Canu & Bassler; 68718 (2), syntypes of *Notoplagioecia farringdonensis* Canu & Bassler.

DESCRIPTION. Zoarium dendroid with slightly compressed branches (Figs 63–66), averaging about 2–3 mm in diameter, circular to elliptical in transverse section, bifurcating more-or-less in the plane of compression, successive bifurcations subparallel. Zooecia are budded from a short median lamina (Fig. 69), which is orientated parallel to the plane of branch compression, and open around the entire perimeter of the branch. Branch growth tips are bluntly conical. The encrusting colony base (Fig. 68) is probosciniform, generally curved, and lacks bifurcations. With a single possible exception, each base gives rise to only one erect stem; cf. Walter (1985) who figures (pl. 5, fig. 2) the base of a colony from the Valanginian of the Jura which apparently bifurcates and gives rise to several erect stems.

Autozooecia are moderately large and arranged in irregular verticels (Fig. 66B) or in approximate quincunx, about 12 zooecia in a circumference of the branch. Frontal walls are flat to slightly convex, about twice as long as wide, with circular pseudopores at a density of about 1200 per mm^2. Apertures usually have low rims, although moderately well developed peristomes occur in a few specimens (e.g. peristomes 0·5 mm long are present in autozooecia on the base of D53698). Autozooecial apertures are subcircular, large, and occasionally occluded by terminal diaphragms. The ancestrula (Fig. 68A) is large (1·2 mm long) with a very wide protoecium (0·5 mm or more).

Gynozooecia (Fig. 67) have subtriangular, well-inflated distal frontal walls indented slightly by autozooecial apertures, and have small, transversely elongate ooeciopores.

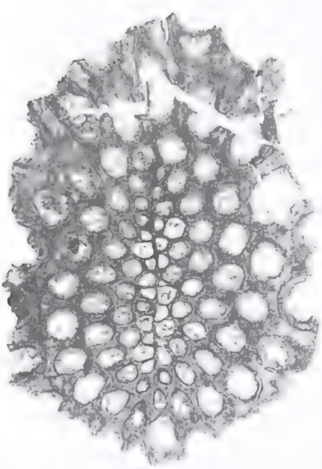
MEASUREMENTS. TAM, 0·10–0·16 mm; TPM, 0·20–0·28 mm; FWL, *c.* 0·65 mm; FWW, *c.* 0·35 mm; GTL, 1·20–2·00 mm; GW, 0·90–1·20 mm; TOSM, 0·20 mm; LOSM, 0·13 mm.

REMARKS. *Cardioecia neocomiensis* has a long synonomy which reflects the wide distribution of the species in the Valanginian to Aptian of Europe.

Canu & Bassler (1922, 1926) described three new species from Faringdon: *Notoplagioecia farringdonensis, Cardioecia faringdonensis*, and *C. pauper*. These were founded on very slight differences and are all regarded as junior synonyms of *C. neocomiensis* (d'Orbigny, 1853). In general, specimens of *C. neocomiensis* from Faringdon have slightly broader branches and thicker peristomes than specimens from argillaceous facies of the Neocomian (e.g. BM(NH) D53146 from the Hauterivian of Lincolnshire). These variations are regarded as ecophenotypic responses of no significance at species level; Flor (1972) found similar branch width variations in the vinculariiform cyclostomes *Spiropora verticellata* and *Entalophora proboscoidea*.

The species name *sanctacrucensis* was introduced by Walter (1967) for *Mesenteripora [Bidiastopora] neocomiensis* (d'Orbigny, 1853: 800; pl. 784, figs 9–11), to avoid hononymy with *M. [Mesenteripora] neocomiensis* (d'Orbigny, 1853: 808; pl. 756, figs 7–9). We regard the new name as superfluous, the former species having been transferred previously to *Cardioecia* by Canu & Bassler (1922).

C. neocomiensis is one of the most common species present at Faringdon. The rather robust branches are an adundant component of sediment samples, and the encrusting colony bases are also comparatively common, some detached from their substrates, but others encrusting shell material, sponges, other bryozoans or pebbles.



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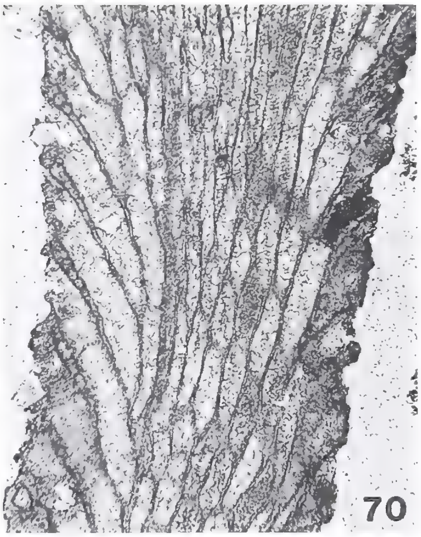

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Figs 69–70 Thin sections. Fig. 69, *Cardioecia neocomiensis* (d'Orbigny), USNM 69893f, syntype of *C. faringdonensis* Canu & Bassler, thick transverse section showing budding lamina, × 29. Fig. 70, *Ceata granulata* (Canu & Bassler), BM(NH) D55141, oblique longitudinal section showing shallow angle of intersection between zooecia on the left and colony surface, × 32.

Genus *CEATA* Strand, 1928

TYPE SPECIES. *Cea rustica* d'Orbigny, 1854, by subsequent designation of Bassler, 1935; Senonian of Vendôme, France.

REMARKS. *Ceata* was proposed by Strand (1928) to replace *Cea* d'Orbigny, 1854, a junior homonym of a hymenopteran genus. It is seemingly a plagioeciid with narrow bifoliate erect branches and trumpet-shaped zooecial tubes which intersect the colony surface at an acute angle. There is some doubt as to whether the type species of this genus has pseudoporous frontal walls of the kind which are visible in well-preserved specimens of *Ceata granulata* (Canu & Bassler) from Faringdon. If not, the Faringdon species may have to be reassigned.

RANGE. Barremian to Senonian.

Ceata granulata (Canu & Bassler, 1926) Figs 70–74

1926 *Cea granulata* Canu & Bassler: 49; pl. 5, figs 6–14; text-fig. 23A–B.

non 1975 *Cea granulata* (Canu & Bassler); Walter *et al*: 108; pl. 9, figs 14–15 [=*Poriceata ardescensis* Walter, 1983].

1981 *Ceata granulata* (Canu & Bassler) Voigt: fig. 1h.

1983 *Ceata granulata* (Canu & Bassler); Walter: pl. 1, figs 1–2.

LECTOTYPE. USNM 69899c, the specimen figured by Canu & Bassler (1926: pl. 5, figs 13–14) is here chosen as the lectotype.

PARALECTOTYPES. USNM 69899a (Canu & Bassler 1926: pl. 5, figs 9–10), 69899b (pl. 5, figs 7–8), 69899d (pl. 5, figs 11–12). There is also a thin section but this bears little resemblance to the section shown by Canu & Bassler in their text-figure 23.

OTHER MATERIAL. BM(NH) D55082 (2), D55086, D55140, D55141 (4 thin sections), D55142 (4), D55143 (sample), Little Coxwell Pit, Thomas Colln; D55083–4, D55139, D55144 (sample), Little Coxwell Pit, Pitt Colln; D55085, ? locality, Pitt Colln; D55145, Little Coxwell Pit, Davis Colln; D55146 (6), ?Little Coxwell Pit, Cleevely Colln; D55147, Curry Colln.

DESCRIPTION. Zoarium erect, consisting of compressed branches which bifurcate in the plane of the compression, though with successive bifurcations somewhat subparallel owing to torsion of the branches. A median budding lamina occupies the centre of the branches which are 1–2 by 0·8–1·0 mm in diameter. Ill-defined maculae with low densities of zooecial apertures have been observed (cf. *Heterohaplooecia* Voigt & Viaud, 1983, and *Plagioecia spissa*, p. 90).

Autozooecia are long trumpet-shaped tubes which intersect the colony surface at a low angle (Fig. 70). In well-preserved specimens (Figs 71, 73) autozooecial frontal walls ('facettes' of Canu & Bassler, 1926) are present which are pseudoporous (*c*. 1800 pseudopores per mm^2) and apparently very thin. Apertures are circular in zooecia with frontal walls (Fig. 73B), closely packed, and have a slightly raised rim ('salient peristome'). In the majority of specimens, however, autozooecial frontal walls are absent (probably owing to mechanical abrasion but possibly primary) and the zooecia have 'false' apertures (Fig. 72B) which are polygonal (often hexagonal or pentagonal) and about 0·15 mm in diameter.

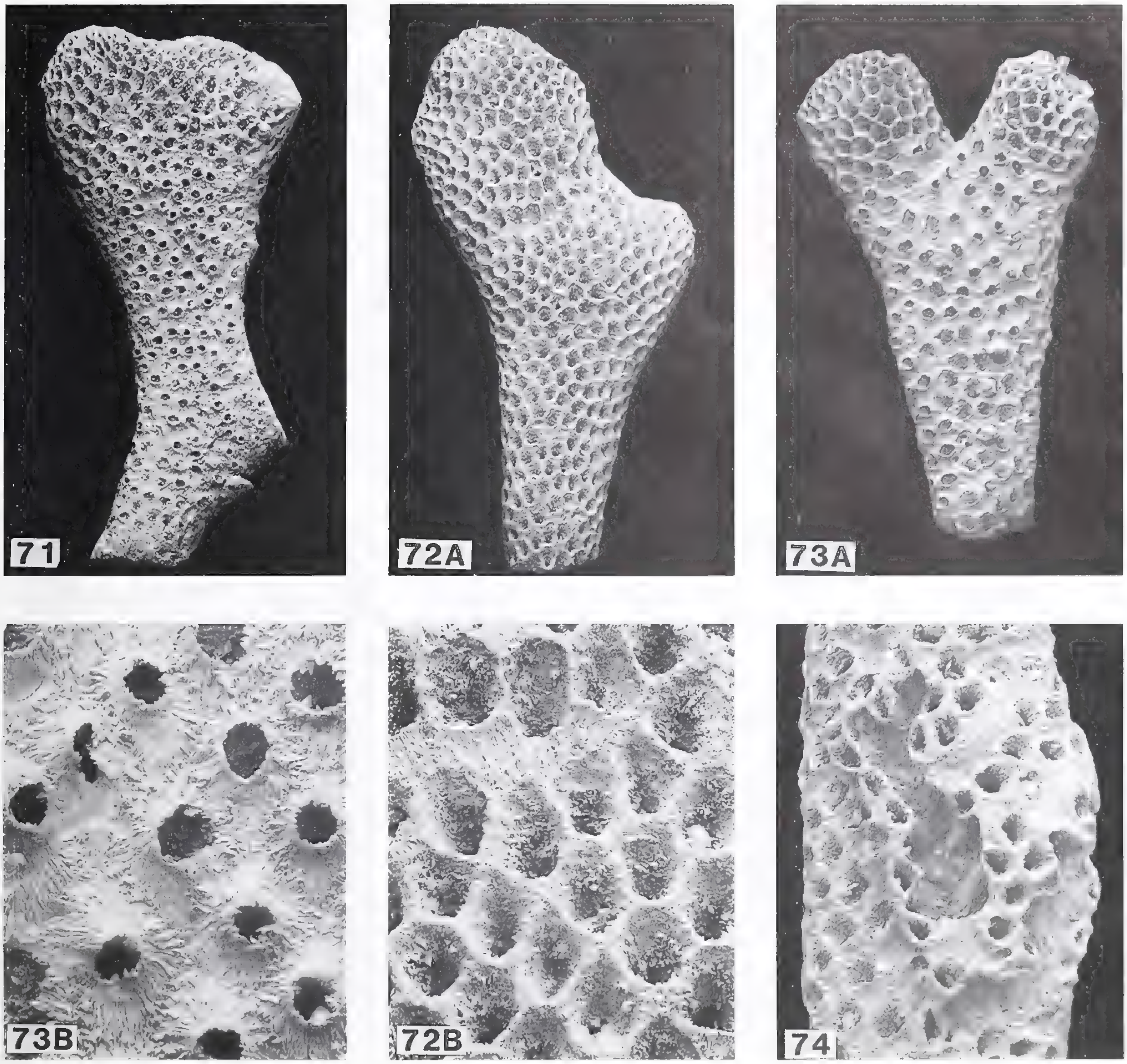
Gynozooecia (Fig. 74) are uncommon and all known examples are damaged. The bulbous distal part of the gynozooecium has two digitate lateral lobes strongly indented by surrounding autozooecia, which extend well distally of the median ooeciopore. The ooeciopore is apparently transversely elongate and small.

MEASUREMENTS. TAM, 0·08 mm; GDL, *c*. 2·3 mm; GW, *c*. 1·0 mm; TOPM, 0·04 mm.

REMARKS. Although branch fragments of this species are abundant at Faringdon, the colony base is unknown. The great majority of specimens are devoid of their zooecial frontal walls. Specimens are most easily confused with *Cardioecia neocomiensis* but are generally less robust.

Genus *MESENTERIPORA* Blainville, 1830

TYPE SPECIES. *Mesenteripora michelini* Blainville, 1830, by original designation; Bathonian of Normandy, France.



Figs 71–74 *Ceata granulata* (Canu & Bassler). Fig. 71, USNM 69899c, **lectotype** (herein selected), with autozooecial frontal walls intact, × 10. Fig. 72, USNM 69899a; 72A, branch with autozooecial frontal walls missing, × 11; 72B, obliquely orientated autozooecia lacking frontal walls, × 53. Fig. 73, BM(NH) D55086; 73A, bifurcating branch, × 12; 73B, circular autozooecial apertures, × 57. Fig. 74, BM(NH) D55084, broken gynozooecium, × 30.

REMARKS. *Mesenteripora* is a plagioeciid genus with erect, foliaceous colonies which are bilamellar, the zooecia budding from both sides of a median budding lamina. In the type species, colonies have tightly folded sinuous fronds, and the gynozooecium is subtriangular in outline (see Walter 1970). Neocomian species of the genus have been revised by Walter (1985).

RANGE. Pliensbachian to Recent.

?Mesenteripora campicheana (d'Orbigny, 1853) Fig. 75

1853 *Bidiastopora campicheana* d'Orbigny: 800; pl. 784, figs 6–8.

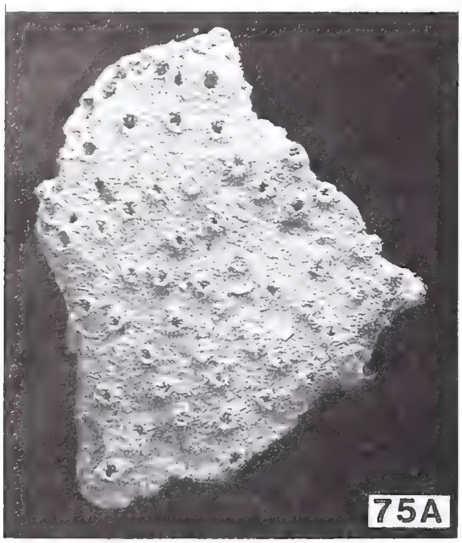
1985 *Mesenteripora campicheana* (d'Orbigny) Walter: 10; pl. 1, figs 1–9; pl. 9, figs 6–7.

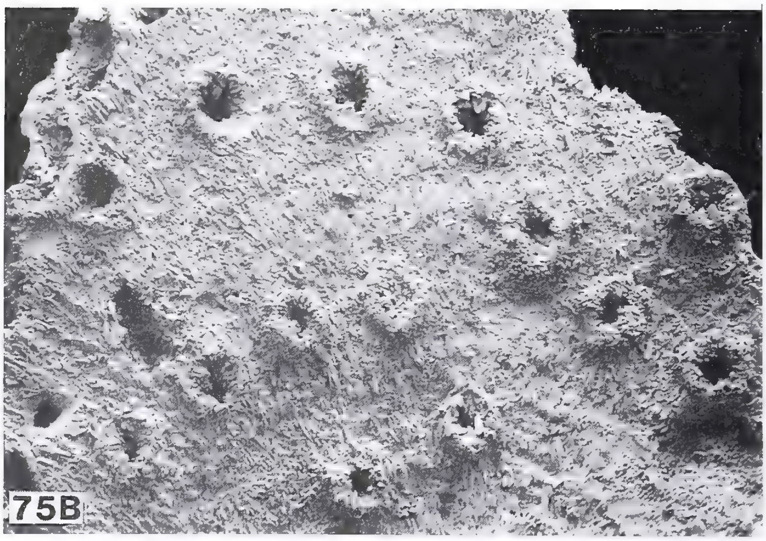
MATERIAL. BM(NH) D55441, Little Coxwell Pit, Davis Colln.

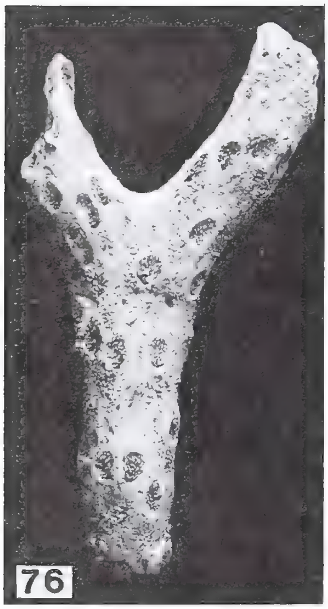
DESCRIPTION. A single poorly-preserved fragment (2×3 mm) of a thin bilamellar frond about 0·3 mm in thickness (Fig. 75A). The autozooecia are immersed, and have apertures which are circular to longitudinally elongate with a slightly raised peristome (Fig. 75B). No gynozooecia are preserved; in specimens described by Walter (1985), the gynozooecia are boomerang-shaped with lateral lobes extending distally of the ooeciopore.

MEASUREMENTS. TAM, mean 0·08 mm; TPM, mean 0·15 mm.

REMARKS. The absence of gynozooecia precludes certain determination of this specimen which is, however, worthy of


75A


75B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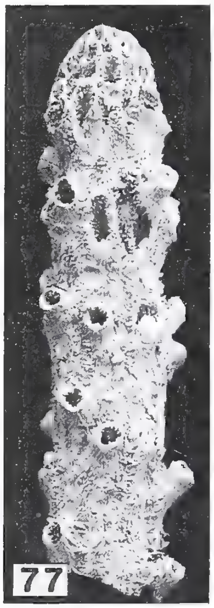
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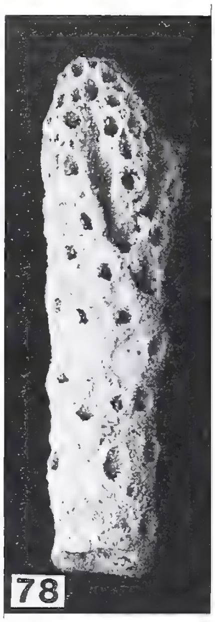
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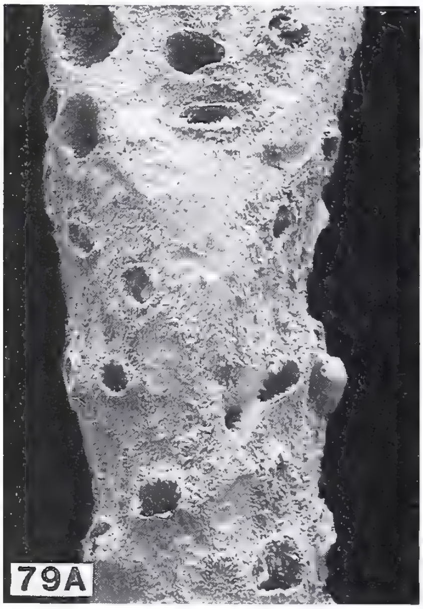
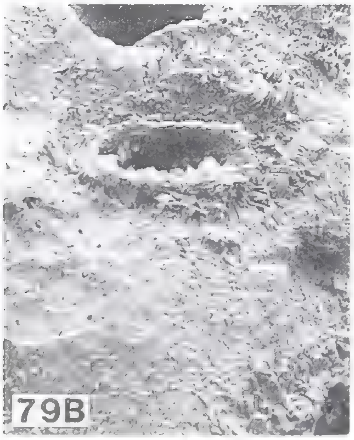
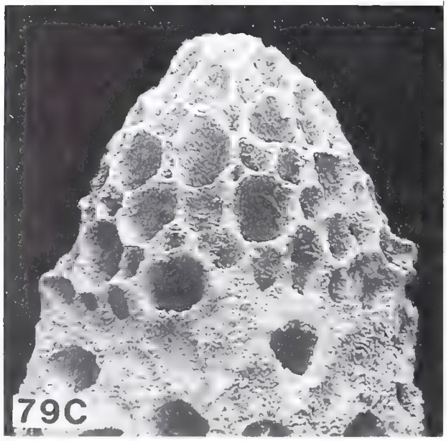

79A


79B


79C

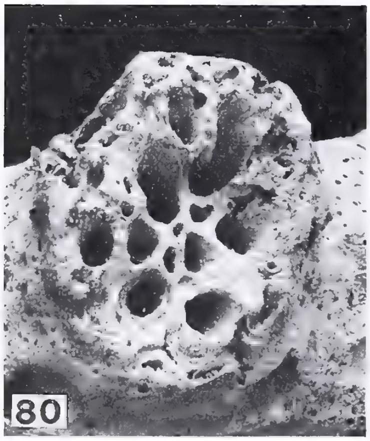

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Fig. 75 ?*Mesenteripora campicheana* (d'Orbigny), BM(NH) D55441; 75A, fragment of bifoliate frond, × 22; 75B, autozooecia, × 60.

Figs 76–80 *Entalophoroecia quadripartita* (Canu & Bassler). Fig. 76, USNM 69852b, paralectotype, × 24. Fig. 77, BM(NH) D55092, × 32. Fig. 78, BM(NH) D55093b, branch fragment with worn gynozooecium, × 22. Fig. 79, BM(NH) D55163; 79A, gynozooecium, × 53; 79B, ooeciopore, × 134; 79C, growth tip (small buds are probably kenozooecia), × 60. Fig. 80, BM(NH) D55093a, fractured branch, × 90.

note in being the only foliaceous tubuloporine recorded from Faringdon.

Genus *ENTALOPHOROECIA* Harmelin 1974*b*

TYPE SPECIES. *Tubulipora deflexa* Couch, 1844, by original designation; Recent.

REMARKS. *Entalophoroecia* was proposed to accommodate some living tubuloporine species (see Harmelin 1974b, 1976; Hayward & Ryland 1985) of a type previously assigned to *Entalophora* Lamouroux but differing from this genus (type species *Entalophora cellarioides* Lamouroux from the Bathonian, see Walter 1970) in not having an axial canal. Colonies of the type species of *Entalophoroecia* possess extensive, probosciniform encrusting bases and complexly interlobed gynozooids with circular ooeciopores on the erect branches.

RANGE. Cretaceous to Recent (this range is highly tentative pending re-evaluation of the diverse species of vinculariiform cyclostomes found in Mesozoic and Cenozoic sediments).

Entalophoroecia quadripartita (Canu & Bassler, 1926)

Figs 76–80

1926 *Clinopora quadripartita* Canu & Bassler: 12; pl. 29, figs 8–11.

LECTOTYPE. USNM 69852a, figd by Canu & Bassler (1926: pl. 29, figs 8, 10, 11), is here chosen as lectotype.

PARALECTOTYPE. USNM 69852b, figd by Canu & Bassler (1926: pl. 29, fig. 9). Only the distal part of this specimen remains; the specimen as figured is considered by A. H. Cheetham (personal communication) to be possibly parts of two specimens glued together.

OTHER MATERIAL. BM(NH) D55092, D55166 (2), Davis Colln; D55123, D55165 (4), Little Coxwell Pit, Davis Colln; D55093 (6), D55157 (sample), D55158 (sample), D55167 (3), D55169 (10), Little Coxwell Pit, Elliott Colln; D55159 (sample), D55160 (sample), D55161 (6), D55162, D55163, D55164 (12), Little Coxwell Pit, Thomas Colln.

DESCRIPTION. Zoarium vinculariiform, consisting of narrow (0·3–1 mm diameter) bifurcating branches (Figs 76–78) which may have dilated portions. Branch growth tips are tall cones (Fig. 79C). The colony base is unknown.

Autozooecia are small and slender, their frontal walls bordered by a slightly raised wall and bearing pseudopores at a density of 1300–1900 per mm^2. Apertures are circular, slightly transversely or slightly longitudinally elongate and have short preserved peristomes. In a branch circumference there are generally 6–8 zooecia, increasing to 10–12 in dilated branches. Aperture spacing and arrangement is highly variable.

Kenozooecia, small and of varying shape, are often abundant and are interspersed irregularly between the autozooecia. They may be visible at growth tips as small buds (Fig. 79C).

Gynozooecia (Figs 78–79), usually preserved broken, have a V-shaped distal frontal wall which includes two lateral lobes extending well distally of the median ooeciopore. The ooeciopore is transversely elongate and slit-like (Fig. 79B).

MEASUREMENTS. TAM, 0·06–0·10 mm; TPM, 0·10–0·14 mm; FWW, mean 0·14 mm; TOSM, 0·20 mm; LOSM, 0·06 mm; TOPM, 0·17 mm; LOPM, 0·04 mm.

REMARKS. Canu & Bassler (1926) assigned this species to *Clinopora* Marsson. The type species of this Upper Cretaceous genus, *C. lineata* (Beisel), has the entire branch surface covered with narrow kenozooecia which form lineations parallel to the growth direction. In *E. quadripartita*, however, autozooecial frontal walls are well developed and kenozooecia are scattered irregularly among the autozooecia; assignment of the Faringdon species to *Clinopora* is therefore incorrect.

Although *Entalophoroecia* Harmelin is a more appropriate genus for the reception of this species, some reservations remain in view of the ooeciopore which is circular in the type species of *Entalophoroecia* but distinctly transverse in *E. quadripartita*.

E. quadripartita resembles *Entalophora vassiacensis* d'Orbigny, 1853, redescribed by Walter (1977) from the Aptian of the Gard (France), in general morphology and particularly in the shape of the gynozooecium. Further study may reveal the two species to be synonymous.

The two Neocomian species *Dichospiropora neocomiensis* (d'Orbigny, 1853) and *Bicoronipora reticuloides* (Canu & Bassler, 1926) have colony forms and gynozooecia similar to those of *E. quadripartita* (see Walter 1987*a*). However, *D. neocomiensis* differs from *E. quadripartita* in having the autozooecial apertures arranged in transverse rings, and *B. reticuloides* in having a narrow axial canal within the branches.

Branch fragments of *E. quadripartita* are very common at Faringdon and it is surprising that all authors prior to Canu & Bassler (1926) overlooked the species. It is readily distinguished from all other Faringdon tubuloporine species except *Collapora hillmeri* by the narrowness of the branches. Unequivocal discrimination between *E. quadripartita* and *C. hillmeri* requires the presence of gynozooecia which have lobes extending distally of the ooeciopore only in the former species.

Family **ELEIDAE** d'Orbigny, 1853
(= MELICERITITIDAE Pergens, 1889)

Genus *MELICERITITES* Roemer, 1840

TYPE SPECIES. *Ceriopora gracilis* Goldfuss, 1826, by subsequent designation of Gregory, 1899; Cenomanian of Essen, West Germany.

REMARKS. Melicerititids are unique among cyclostomes in possessing zooids with hinged opercula closing the aperture (see Levinsen 1912). These are calcified structures which are often preserved *in situ*; when missing, the past presence of an operculum can be inferred from the straight proximal edge of the aperture which formed the hinge line of the operculum. In many species polymorphic zooids – eleozooids (Taylor 1985) – with enlarged opercula are developed.

Meliceritites is the only eleid genus known in the Aptian. Species of *Meliceritites* have vinculariiform colonies with autozooecia opening around the entire perimeter of the branches (cf. *Meliceritella*), a single-walled organization (cf. *Foricula*), and eleozooecia either absent or greatly outnumbered by the autozooecia (cf. *Atagma*).

RANGE. Barremian to Maastrichtian.

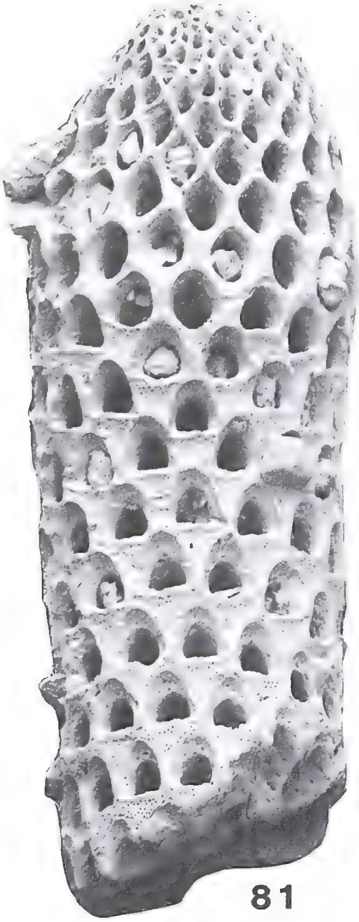


Fig. 81 *Meliceritites gracilis* (Goldfuss), BM(NH) D55288, branch with growth tip, × 30; see also Fig. 82.

Meliceritites gracilis (Goldfuss, 1827) Figs 81–84

1827 *Ceriopora gracilis* Goldfuss: 35; pl. 10, fig. 11a–c.
1840–1 *Meliceritites (Ceriopora) gracilis* (Goldfuss) Roemer: 18; pl. 5, fig. 13.
?1871 *Meliceritites gracilis* (Goldfuss); Simonowitsch: 66.
non 1887 *Meliceritites gracilis* (Goldfuss); Marsson: 46; pl. 4, fig. 8 [=*M. gothica* Levinsen].
non 1897 *Meliceritites gracilis* (Goldfuss); Canu: 752; pl. 22, figs 1–2.
1899 *Meliceritites gracilis* (Goldfuss); Gregory: 324; fig. 38.
1912 *Meliceritites gracilis* (Goldfuss); Levinsen: 28; figs a, b on p. 29.
1922 *Meliceritites gracilis* (Goldfuss); Canu & Bassler: 83; pl. 13, figs 1–4.
1975 *Meliceritites semiclausa* (Michelin); Walter *et al.*: 109; pl. 10, figs 5–6; text-fig. 8.
1981 *Meliceritites gracilis* (Goldfuss); Voigt: 445; fig. 2j.

MATERIAL. BM(NH) D55287, Little Coxwell Pit, Curry Colln; D55288–9, Little Coxwell Pit, Elliott Colln; D55290–1, Little Coxwell Pit, Whiteley Colln; D55292, Cleevely Colln; D55293–4, Davis Colln.

DESCRIPTION. Colonies are dendroid with moderately thick (1–1·5 mm), bifurcating vinculariiform branches (Fig. 81) which may develop overgrowths through branch collision. Growth tips are rounded conical in shape.

Autozooecia are generally arranged in well-defined transverse rows (Fig. 82), and are rounded diamond-shaped to subhexagonal in frontal outline with pseudoporous frontal walls of relatively small area. Apertures are closely-spaced, large, arched and significantly higher than wide. There is no true opercular shelf, but apertures are flared and may possess a deep distal ledge (Fig. 84A). Opercula (Fig. 84B) are seldom found *in situ*. Apertures are very often occluded by non-pseudoporous diaphragms (Fig. 83), located at the level of flaring, some of which have a central depression and pore.

Gynozooecia are unknown in Faringdon specimens; however, specimens from the U. Barremian of southern France and the Cenomanian of Germany have gynozooecia with bulbous distal frontal walls, longitudinally elliptical to subtriangular in outline, a transversely elongate ooeciopore and an atrial ring.

Eleozooecia are absent.

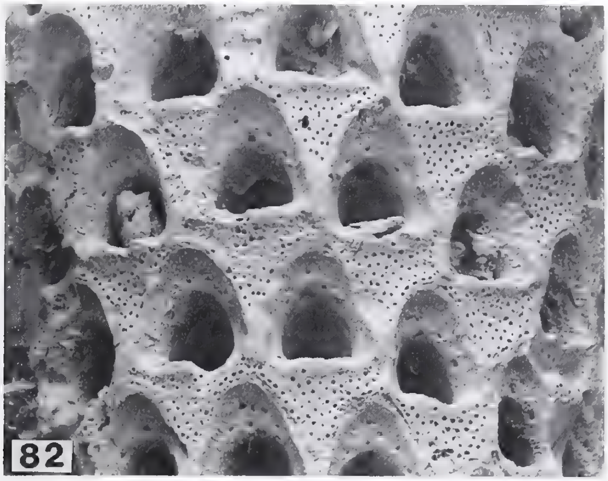
MEASUREMENTS (based on determinations of 10 autozooecia from BM(NH) D55288). FWL, 0·33–0·50 mm; FWW, 0·24–0·29 mm; LAM, 0·21–0·26 mm; TAM, 0·17–0·20 mm.

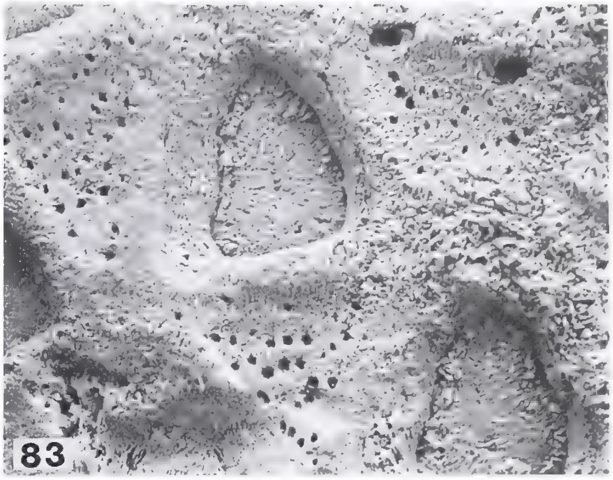
REMARKS. This species has not been previously recorded from Faringdon and is considerably rarer than the three other melicerititids. It is distinguished by the shape of the large autozooecial apertures which are significantly higher than wide.

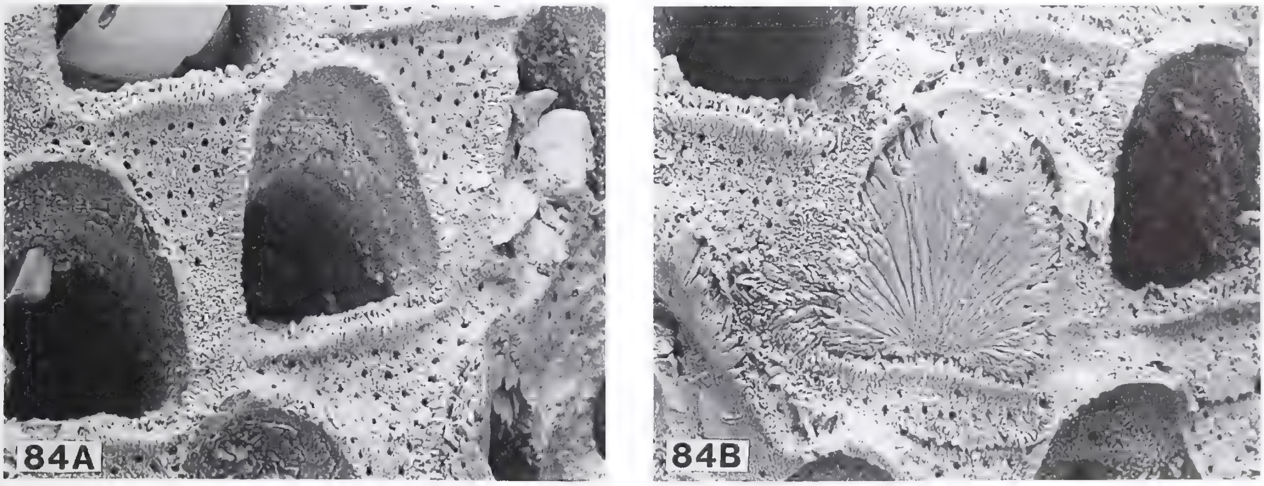
The type locality for *M. gracilis* is the Cenomanian of Essen, West Germany. The species appears to range down into the Upper Barremian, making it one of the oldest known melicerititids. However, populations of differing age are not absolutely identical. Some, though not all, of the specimens from Essen possess autozooecia with platforms extending inwards from the hinge line and perpendicular to the frontal wall (see the 'salpinginid tubuliporate' figured by Boardman *et al.* 1983: fig. 141, 5a–c). Curved, asymmetrical apertures are also a feature of many Essen specimens. Specimens from the Barremian of Nord Serre de Tourre (France) may have tubercles close to the proximolateral borders of the autozooecial apertures. There is also variation in the precise location and obliquity of diaphragms, the area of frontal walls and the dimensions of the autozooecia. Taking this variation into account, it is possible that *Meliceritites upwarensis* Keeping, described from the Aptian of Upware (holotype SM B26098), which closely resembles *M. gracilis* but has larger autozooecia (LAM 0·26–0·29 mm; TAM 0·18–0·23 mm), is a junior synonym of *M. gracilis*.

Meliceritites dendroidea (Keeping, 1883) Figs 85–91

?1853 *Multelea gracilis* d'Orbigny [sic; (Goldfuss)]; d'Orbigny: 645; pl. 739, figs 1–3.
1883 *Entalophora dendroidea* Keeping: 138; pl. 7, fig. 12a, b.
1899 *Meliceritites semiclausa* (Michelin); Gregory: 328 (*partim*); pl. 14, fig. 3 only.
1926 *Lobosoecia semiclausa* (Michelin); Canu & Bassler: 63; pl. 14, figs 12–13.
1926 *Meliceritites semiclausa* Gregory [sic; (Michelin)]; Canu & Bassler: 66; pl. 11, figs 12–13.







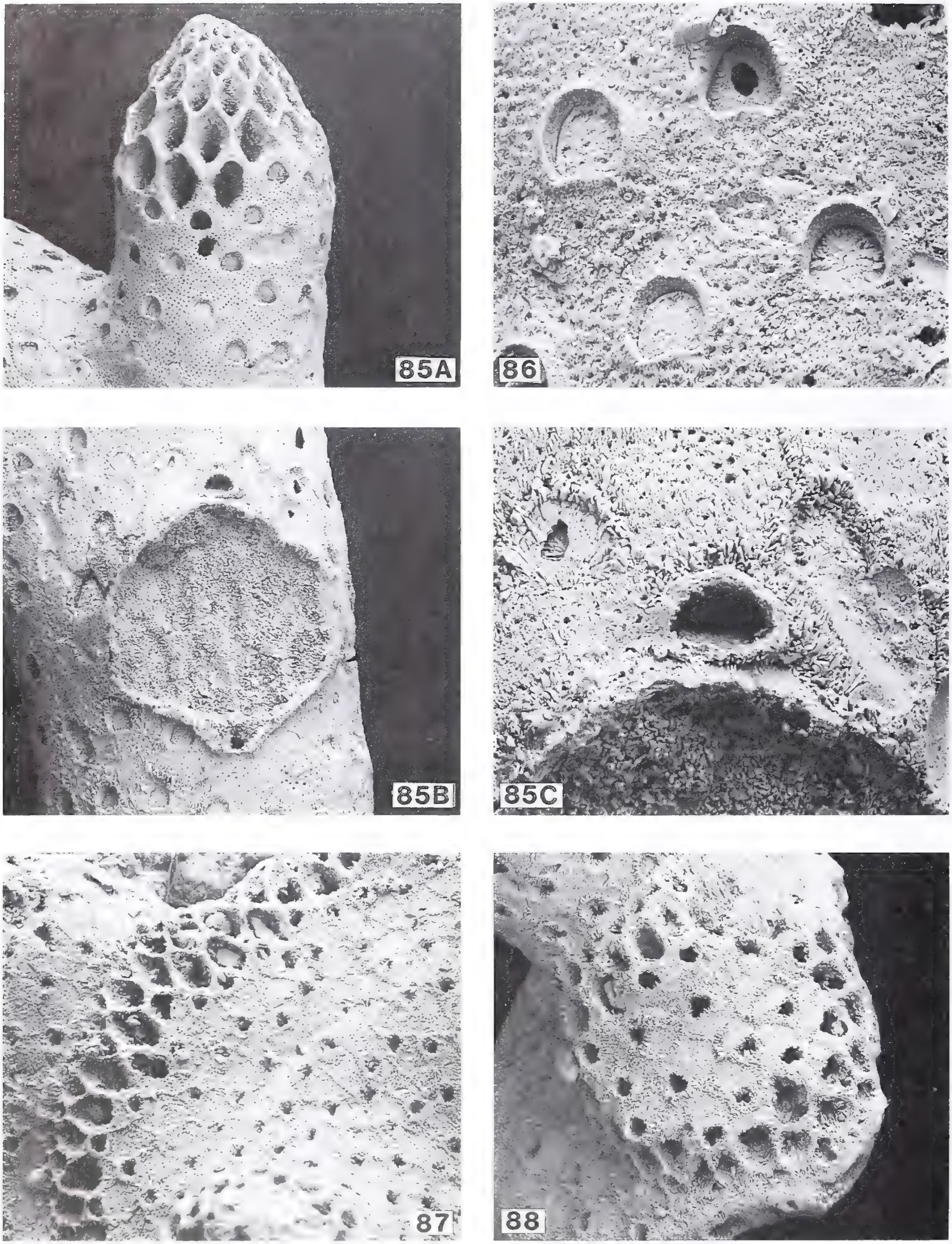
Figs 82–84 *Meliceritites gracilis* (Goldfuss). Fig. 82, BM(NH) D55288, autozooecia, × 69; see also Fig. 81. Fig. 83, BM(NH) D55287, terminal diaphragm covering autozooecial aperture, × 130. Fig. 84, D57392; 84A, open autozooecial aperture in a slightly oblique view, × 180; 84B, operculum, × 185.

non 1974 *Meliceritites semiclausa* (Michelin); Masse & Walter: 192; pl. 36, figs 4–5, 9.
non 1975 *Meliceritites semiclausa* (Michelin); Walter *et al.*: 109; pl. 10, figs 5–6; text-fig. 8.
?1977 *Meliceritites semiclausa* (Michelin); Walter: 328; pl. 1, figs 5, 10.
?1979 *Meliceritites semiclausa* (Michelin); Walter & Clavel: 823; pl. 1, figs 1–2.

MATERIAL. BM(NH) 50781, Morris Colln; 60539, Cunnington Colln (figd by Gregory 1899: pl. 14, fig. 3, who erroneously gave the horizon and locality as Upper Greensand, Warminster); D15051, Treacher Colln; D52153 (sample), D52189–90 (samples), D57706–7 (SEM stub), Little Coxwell Pit, Pitt Colln; D55173 (sample), Thomas Colln; D55174, D55350 (sample), Little Coxwell Pit, Gaster Colln; D55176 (sample), D57648 (sample), Davis Colln; D55177–78 (samples), D55271, D55273 (sample), D55349 (sample), Little Coxwell Pit, Thomas Colln; D55268, Wicklesham Pit (Red Gravels), Taylor Colln; D55269, Little Coxwell Pit, Laurie Colln; D55270 (sample), Little Coxwell Pit, Cleevely Colln; D55272 (sample), Little Coxwell Pit, Curry Colln; D55285 (sample), D57389, Little Coxwell Pit, Elliott Colln.

DESCRIPTION. Colonies are dendroid (Fig. 90) with narrow (0·72–1·17 mm), vinculariiform branches which bifurcate infrequently (internode length 1·4 mm to more than 8·0 mm) and are often slightly sinuous. Branches may anastomose and the resultant concave attachment scars are commonly found in fragmented material. Growth tips have a rounded conical shape (Fig. 85A) and are sometimes occluded. Colony bases may be extensive, giving rise to more than one erect branch. Overgrowths (Figs 87–88) are uncommon in Faringdon specimens (cf. specimens from the Lower Greensand of Upware), except close to the colony base (Fig. 91) where they are apparently formed as a result of frontal budding.

Autozooecia are generally arranged in well-defined transverse rows, and have subhexagonal frontal outlines, their distal parts rounded to accommodate the aperture, with interzooecial walls usually standing a little above the level of the slightly convex, pseudoporous frontal walls. Apertures (Fig. 86) are very small, hemi-elliptical, about as long as wide, and well-rounded distally. A slight distal and lateral apertural rim is present, the hinge line is gently convex without distinct hinge teeth, and there is no appreciable operculum shelf. Diaphragms (Fig. 86) are commonly found just inward of the aperture and vary from sparsely



Figs 85–88 *Meliceritites dendroidea* (Keeping). Fig. 85, BM(NH) D57389; 85A, growth tip, × 42; 85B, gynozooecium with abraded frontal wall, × 62; 85C, ooeciopore, × 218. Fig. 86, BM(NH) 60539, terminal diaphragms (one of which is bored) occluding autozooecial apertures, × 147. Fig. 87, BM(NH) 50781, colony base, × 40. Fig. 88, BM(NH) D57391, frontally-budded overgrowth near colony base, × 55.

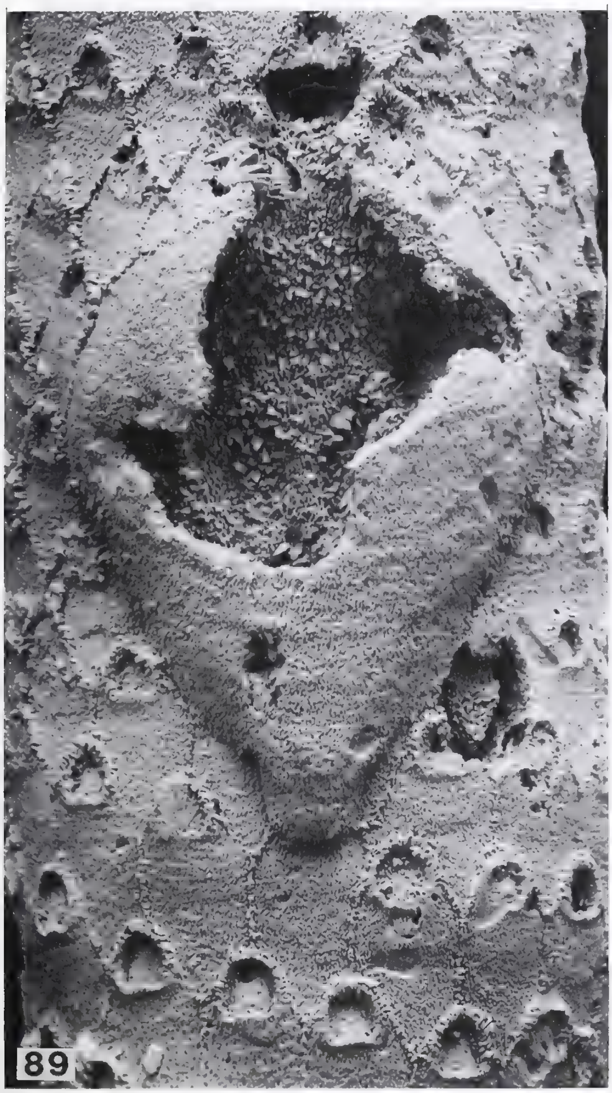


Fig. 89 *Meliceritites dendroidea* (Keeping), BM(NH) D52153, broken gynozooecium, × 69.

pseudoporous to non-pseudoporous, occasionally with a central depression and pore. Opercula are frequently found *in situ*; worn examples have 10–12 pits arranged in a crescent parallel to the lateral and distal edges of the operculum. The inner surfaces of dissected opercula appear to lack distinct sclerites but have a raised marginal shelf.

Eleozooecia have not been observed in Faringdon specimens; however, a specimen from the Aptian Bargate Stone of Kent possesses eleozooecia with apertures of a similar shape to the autozooecia but about twice the size.

Gynozooecia are moderately common. The bulbous distal part of the frontal wall has a longitudinally elliptical to pear-shaped outline (Figs 85B, 89), often with a parallel-sided initial portion leading from the hemi-elliptical parental aperture. Autozooecia and kenozooecia bordering the gynozooecium are often raised. Interzooecial walls of occluded autozooecia are prominent on the floor of abraded gynozooecia (Fig. 85B), but an atrial ring has not been observed. The ooeciopore, situated a little distal of the bulbous part of the gynozooecium, is transversely elliptical (Fig. 85C); in one example it is apparently occluded by a diaphragm.

MEASUREMENTS (autozooecial dimensions from 10 determinations of zooecia in one colony; gynozooecial dimensions from measurements of 6 gynozooecia). FWL, 0·32–0·39 mm; FWW, 0·18–0·23 mm; LAM, 0·08–0·09 mm; TAM, 0·08–0·09 mm; GTL, 1·11–1·58 mm; GDL, 0·92–1·35 mm; GW, 0·75–0·93 mm; LOPM, 0·05 mm; TOPM, 0·08–0·09 mm.

REMARKS. *Meliceritites dendroidea* is a very common species at Faringdon and can be distinguished from the other melicerititids by the small size of the apertures and the narrow diameter of the branches.

The species is usually incorrectly cited as *Meliceritites semiclausa* (Michelin), a species from the Cenomanian of Le Mans which has larger autozooecia, abundant eleozooecia with funnel-shaped apertures, and branches with narrow axial canals.

Faringdon specimens of *Meliceritites dendroidea* (Keeping) have slightly smaller autozooecia than the holotype (SM B26086) from the Lower Greensand of Upware, but very few autozooecia can be measured in this poorly-preserved specimen and those that are measurable all come from an overgrowth close to the colony base. It is possible that the *Multelea gracilis* (Michelin, *non* Goldfuss) of d'Orbigny (1853), described from the Albian of Grandpré, is a synonym of *Meliceritites dendroidea*. However, autozooecia measured from specimens in the d'Orbigny Collection (MNHN 6022) have larger frontal walls than either Upware or Faringdon specimens.

Meliceritites cunningtoni (Gregory, 1899) Figs 92–96

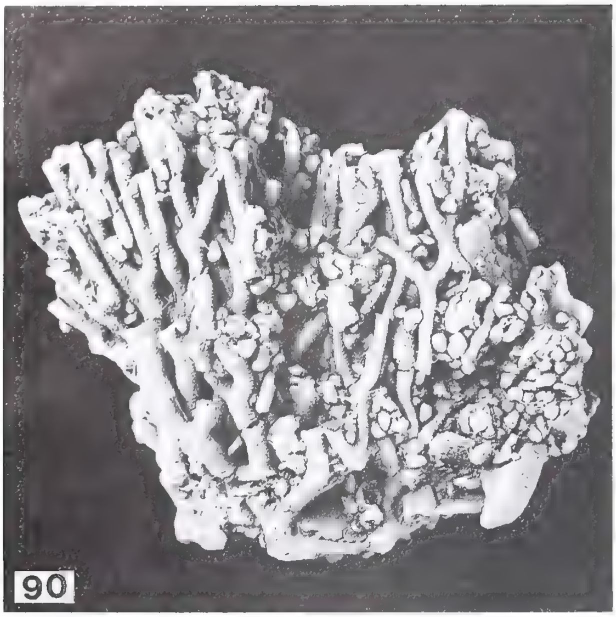
1899 *Nodelea cunningtoni* Gregory : 308; text-figs 35–36.
1926 *Meliceritites cunningtoni* (Gregory) Canu & Bassler: 65; pl. 13, figs 1–8.
1981 *Meliceritites cunningtoni* (Gregory); Voigt: 441; fig. 1e.

LECTOTYPE. BM(NH) D5137, Cunnington Colln, figured by Gregory (1899: text-fig. 35) is here selected as the lectotype. Faringdon Sponge Gravel, Faringdon.

PARALECTOTYPES. BM(NH) D5131, D5132, D5137, Faringdon, Cunnington Colln. The remaining specimens (syntypes) listed by Gregory (1899: 309) are either worn and indeterminate or comprise mixed samples of vinculariiform cyclostomes.

OTHER MATERIAL. BM(NH) D52191 (sample), D55258 (sample), D55259 (sample), D55260–1, D57390, D57702 (SEM stub), Little Coxwell Pit, Pitt Colln; D55169 (sample), Little Coxwell Pit, ?colln; D55170 (sample), D55172 (sample), Little Coxwell Pit, Thomas Colln; D55171 (sample), D57386, D57649 (sample), Davis Colln; D55262 (sample), Little Coxwell Pit, Gaster Colln; D55263 (sample), Little Coxwell Pit, Thomas Colln; D55264 (sample), Cleevely Colln; D57703 (SEM stub), Little Coxwell Pit, ?Colln. USNM 69917, 7 fragments mounted on a card, figd by Canu & Bassler (1926: pl. 13, figs 1–8).

DESCRIPTION. Colonies are dendroid with relatively thick (1·45–2·0 mm), straight or slightly curved, vinculariiform branches (Fig. 92A) which bifurcate at irregular intervals (internode lengths of 0·36 mm to over 14 mm have been observed), successive bifurcations generally occurring in planes at 90°. The colony base has not been observed. Occasional overgrowths seem to be the result of branch collisions. Branch growth tips are rounded dome-shaped or



Figs 90–91 *Meliceritites dendroidea* (Keeping), optical photographs. Fig. 90, BM(NH) D55268, well-preserved bushy colony, × 1·9. Fig. 91, BM(NH) 50781, colony base (lower right) encrusting a pebble together with various other species, × 1·8.

high rounded cones (Fig. 92A); sometimes the immature zooecia at the growth tip are occluded by pseudoporous terminal diaphragms at a level slightly proximal of the outer ends of their interzooidal walls.

Autozooecia, generally arranged in well-ordered transverse rows (Fig. 92B), are subhexagonal in frontal outline and have small frontal walls and large, closely-spaced apertures which are more-or-less hexagonally packed. Apertures (Fig. 92D) are flared, hemielliptical, a little wider than high, well-rounded distally, and have slightly convex hinge lines. Rarely a concentric inner rim occurs within the aperture, indicating intramural budding (Fig. 92B). Opercula (Fig. 95) are frequently preserved *in situ*; they have a microstructure of coarse crystallites in a typically melicerititid fan-like arrangement, and a crescent of pits close to the free edges. The inner side of opercula, revealed by dissecting out individual opercula or observing abraded *in situ* opercula, has a pair of thick, apparently hollow, inward-sloping sclerites continuous with a knob-like process which extends proximally of the hinge line. Zooecia commonly have only the proximal part of the operculum preserved (Fig. 96), a style of preservation which is rarely found in species of melicerititids and suggests a strong articulation between the hinge line and operculum. Apertures may be occluded by sparsely to densely pseudoporous diaphragms situated proximally of the outer edge of the aperture, sloping distally outwards, often irregular and sometimes possessing a central depression; such diaphragms may be observed beneath the operculum in zooecia with fractured opercula (Fig. 92C).

Gynozooecia (Figs 93–94) are rare, small, and have a subtriangular surface outline, about as broad as long, with a bulbous distal frontal wall which is seldom preserved. The ooeciopore, located distally of the dilated part of the gynozooecium, is small (0·07 mm in diameter), circular and borne on a proximally-reflexed ooeciostome (Fig. 93). An atrial ring (see Levinsen 1912) has not been observed. Abraded gynozooecia reveal the prominent hexagonal interzooidal walls of the zooecia beneath the floor of the gynozooecium (Fig. 94).

Measurements (autozooecial dimensions from ten determinations on the lectotype; gynozooecial dimensions from three gynozooecia in separate colonies). FWL, 0·41–0·50 mm; FWW, 0·27–0·33 mm; LAM, 0·05–0·18 mm; TAM, 0·17–0·21 mm; GTL, 1·20–1·38 mm; GDL, 1·05–1·23 mm; GW, 1·11–1·32 mm.

Remarks. This species is abundant at Faringdon but is unknown elsewhere. It is distinguished from the three other Faringdon melicerititids by the larger size of the apertures and the greater diameter of the branches. The apertures are also very closely spaced, and the frontal walls reduced in area. The occurrence of a process extending proximally of the hinge line on the inner side of the operculum is seemingly unique among melicerititid species.

Canu & Bassler (1926: pl. 13, figs 4–5) illustrate apparent eleozooids ('eleocellaria') in *M. cunningtoni*. These are in fact abraded autozooecia in which remnants of the hinge lines resemble partially-preserved pivotal bars of cheilostome avicularia, the analogues of melicerititid eleozooids (see Taylor 1985). True eleozooids are absent from *M. cunningtoni* and Faringdon populations of all melicerititid species.

Meliceritites transversa Canu & Bassler, 1926

Figs 97–101

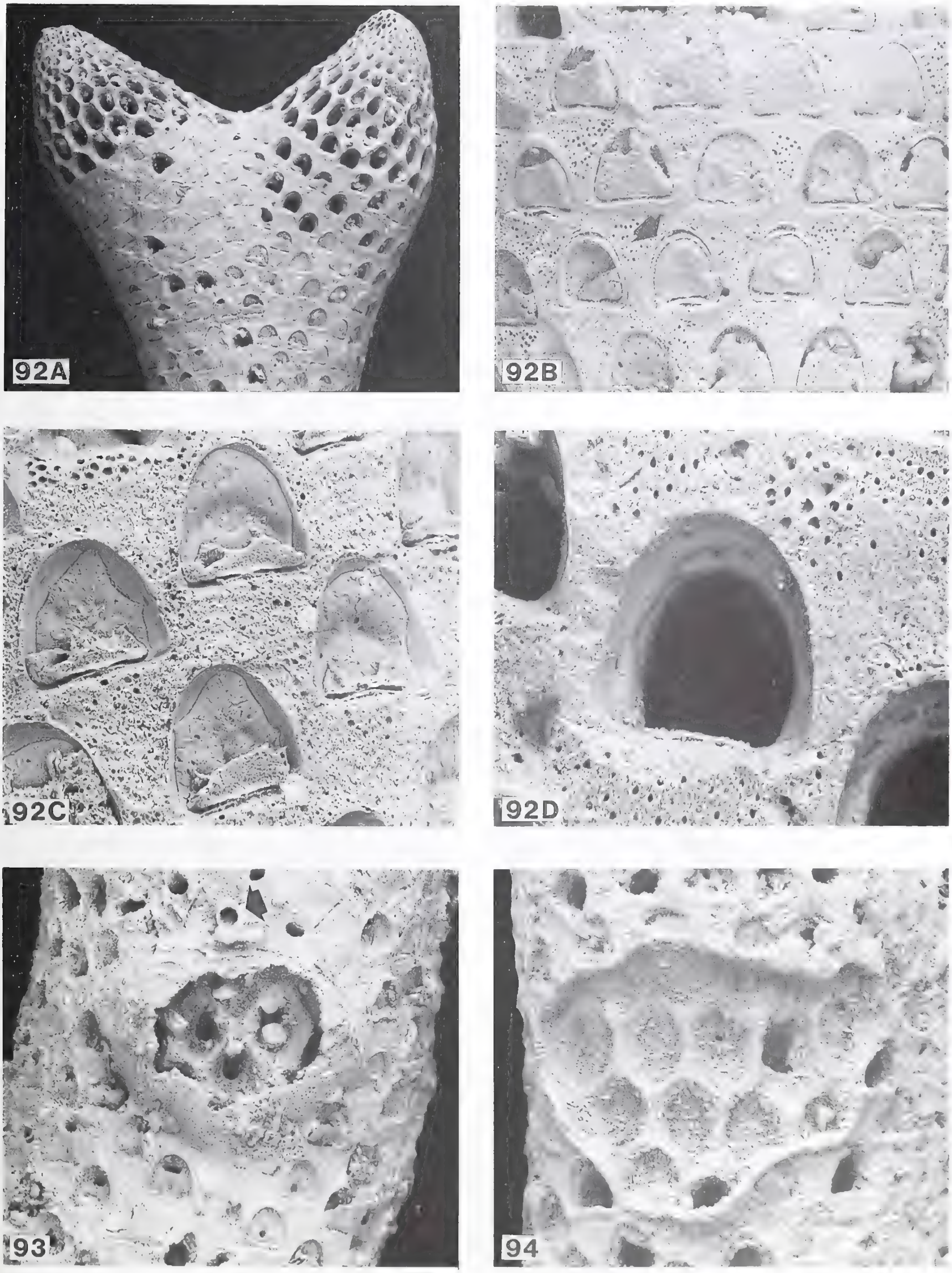
1926 *Meliceritites transversa* Canu & Bassler: 64; pl. 12, figs 1–12.

1981 *Meliceritites haimeana* (d'Orbigny); Voigt: 441; fig. 1f.

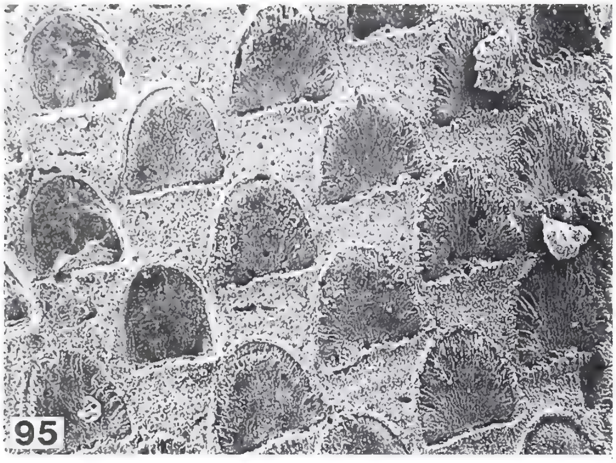
Lectotype. USNM 69916a, figd by Canu & Bassler (1926: pl. 12, figs 2, 3, 6) is here designated as lectotype.

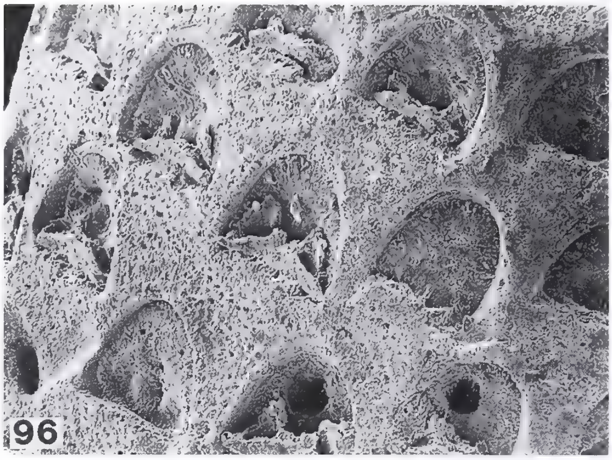
Paralectotypes. USNM 69916b-i, the remaining specimens on the card of syntypes.

Other material. BM(NH) D52154 (sample), D52156 (sample), D55275 (sample), D55281–2, D55284, D57704–5



Figs 92–94 *Meliceritites cunningtoni* (Gregory). Fig. 92, BM(NH) D57390; 92A, bifurcating branch with growth tips, × 18; 92B, autozooecia, some having intramural buds (arrowed), × 75; 92C, broken opercula and terminal diaphragms, × 137; 92D, open autozooecial aperture, × 250. Fig. 93, BM(NH) D57386, gynozooecium (ooeciopore arrowed), × 42. Fig. 94, BM(NH) D55260, gynozooecium lacking frontal wall revealing hexagonal outlines of zooecia covered by the gynozooecium, × 46.





Figs 95–96 *Meliceritites cunningtoni* (Gregory), secondary electron images of coated specimens. Fig. 95, BM(NH) D57703, operculate autozooecia, × 52. Fig. 96, BM(NH) D57702, oblique view of autozooecia with fractured opercula showing apparently hollow sclerites, × 78.

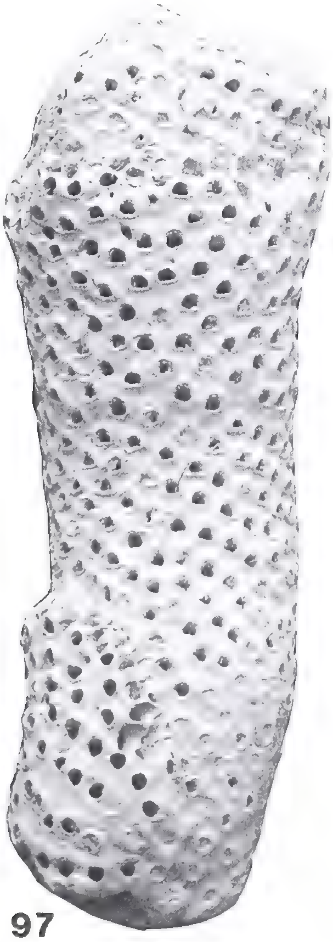


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Fig. 97 *Meliceritites transversa* Canu & Bassler, USNM 69916b, paralectotype, × 17.

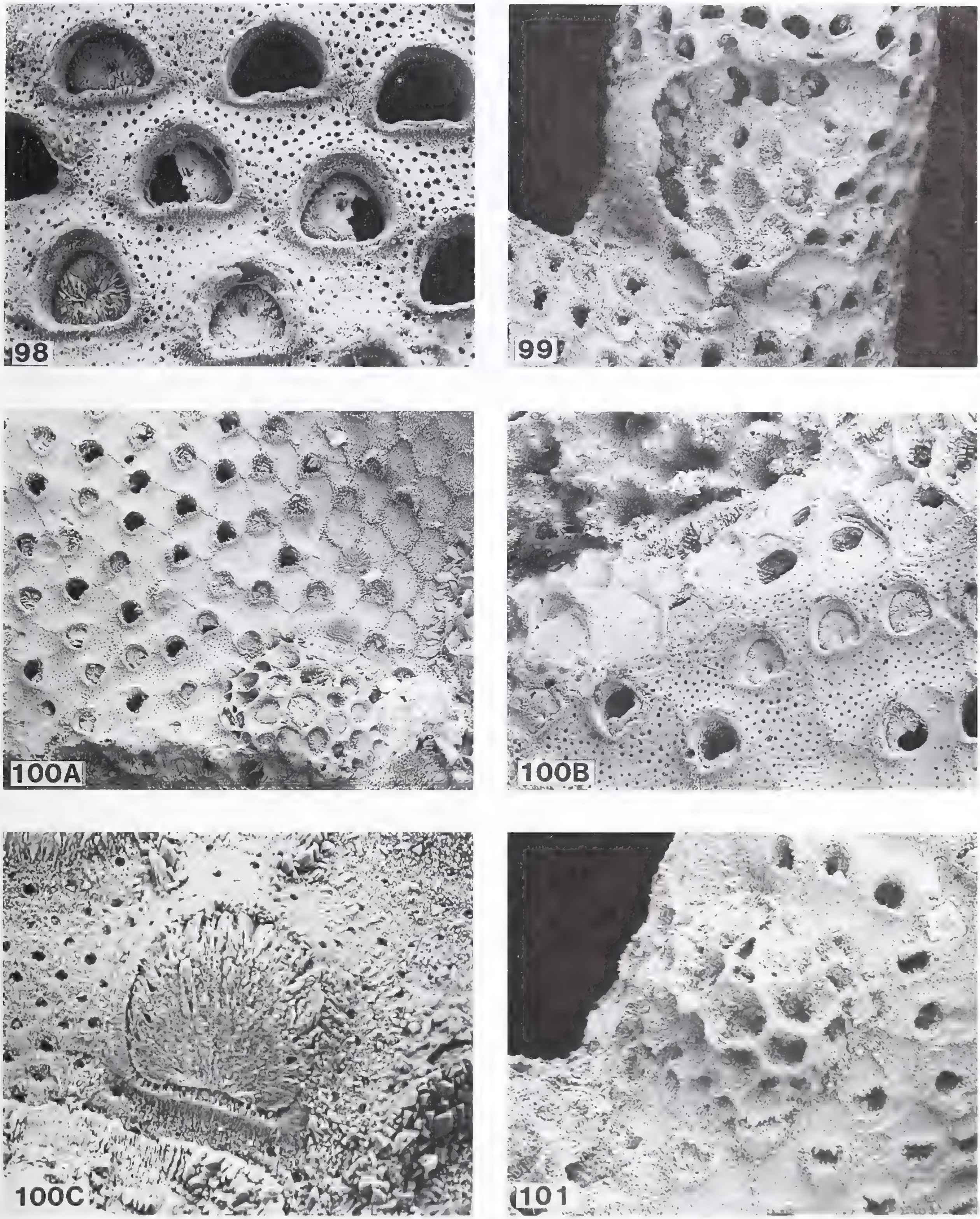
(SEM stub), Little Coxwell Pit, Pitt Colln; D55175, D55182–4 (samples), D55283, D57387, Little Coxwell Pit, Gaster Colln; D55185–7 (samples), D55279 (sample), D57388, Little Coxwell Pit, Thomas Colln; D55191–2, Bowler's Pit, Pitt Colln; D55276–7 (sample), Little Coxwell Pit, Curry Colln; D55278 (sample), D55286, Little Coxwell Pit, Elliott Colln; D55280, Cleevely Colln.

DESCRIPTION. Colonies are dendroid with moderately thick (0·9–1·6 mm) vinculariiform branches (Fig. 97) which bifurcate generally at intervals of 3–6·5 mm and sometimes abruptly become thinner following a bifurcation. Branch growth tips are rounded to conical. Overgrowths are common; some apparently arose from the colony base, but others arose on the surface of the erect branches. Overgrowths form by frontal budding (Fig. 101), successive overgrowths sometimes having their origins directly above one another. The colony base (Fig. 100) is bereniciform, gives rise to a single erect branch, and may have an occluded growth margin (Fig. 100B) and occasional kenozooecia.

Autozooecia are usually arranged in well-defined transverse rows, and have a subhexagonal frontal outline with the interzooecial walls standing up slightly above the level of the pseudoporous frontal wall. Autozooecia in overgrowths and on the colony base are longer and narrower than those in erect branches (compare Figs 100A and 98). Apertures are moderately large, usually slightly broader than high, hemi-elliptical, well-rounded distally, and have a distinct, thickened apertural rim and a hinge line with two prominent teeth (Fig. 98). Terminal diaphragms are sometimes present proximally of the apertural rim; they vary from densely pseudoporous to non-pseudoporous, and may possess a central depression and pore (Fig. 98). The opercular shelf is absent or extremely slight. Opercula are very rarely preserved *in situ*; the only observed examples (Fig. 100C) are recrystallized but appear to have a crescent of pits, as is typical for melicerititids.

Gynozooecia (Fig. 99) are rare but when present occur in multiples. The bulbous distal frontal wall has a subtriangular outline shape, broader than long. Interzooecial walls of occluded zooecia are prominent on the floor of gynozooecia whose roofs have been removed. The ooeciopore is situated slightly distally of the dilated part of the gynozooecium, and is small and transversely elongate. An atrial ring does not seem to occur.

MEASUREMENTS (autozooecial dimensions from ten determinations of zooecia from an erect branch and ten determinations of zooecia in an overgrowth in one colony; gynozooecial dimensions from four gynozooecia in two colonies). FWL, 0·30–0·39 mm; FWW, 0·17–0·26 mm; LAM, 0·09–0·12 mm; TAM, 0·11–0·14 mm; GTL, 0·92–1·20 mm; GDL, 0·81–1·10 mm; GW, 1·13–1·50 mm; LOPM, 0·05 mm; TOPM, 0·09 mm.



Figs 98–101 *Meliceritites transversa* Canu & Bassler. Fig. 98, BM(NH) D55284, autozooecia some of which have terminal diaphragms with a central depression and pore, × 115. Fig. 99, BM(NH) D57387, broken gynozooecium, × 44. Fig. 100, BM(NH) D55175, colony base; 100A, basal autozooecia and abortive frontally-budded overgrowth (bottom right), × 40; 100B, occluded growth margin, × 89; 100C, operculum, × 350. Fig. 101, BM(NH) D57388, small frontally-budded overgrowth, × 65.

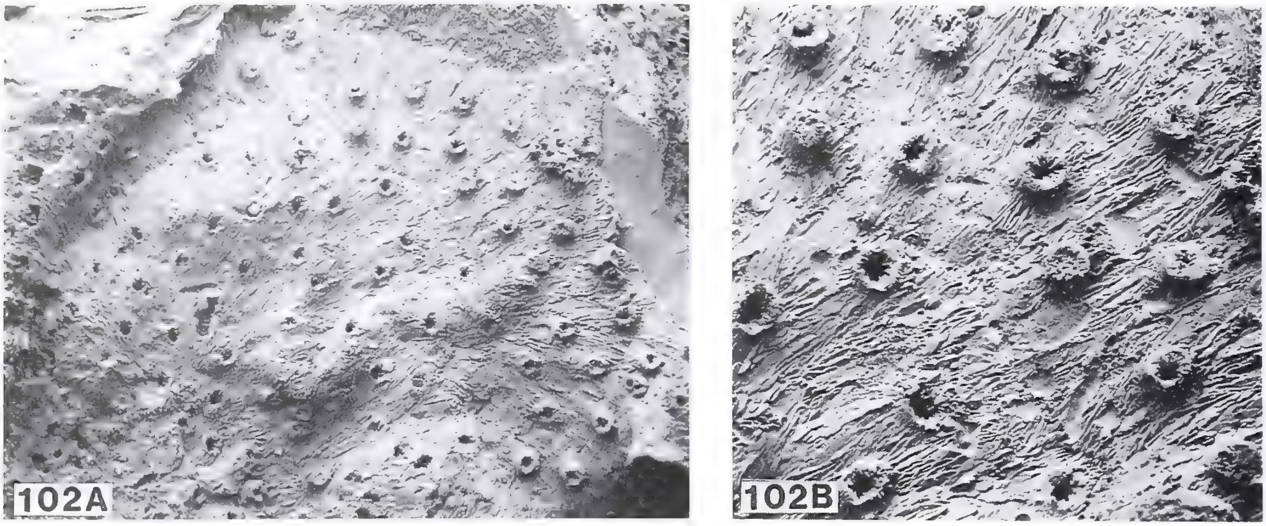


Fig. 102 *'Berenicea' filifera* Canu & Bassler, USNM 69848, holotype; 102A, × 15; 102B, coarsely preserved autozooecia, × 29.

REMARKS. Branch fragments of *M. transversa* are abundant at Faringdon. Zooecial size and branch diameter are intermediate between the two other common Faringdon melicerititids, *M. dendroidea* and *M. cunningtoni*. The species is readily distinguished from the much rarer *M. gracilis* by the well-rounded apertures.

M. transversa has previously been regarded (Walter & Busnardo 1971; Walter *et al.* 1975) as a junior synonym of *M. haimeana* (d'Orbigny), and Voigt (1981) has figured a Faringdon specimen under this latter name. However, the synonymy is not well supported. The specimens of *M. haimeana* figured by d'Orbigny (1853: pl. 617, figs 11-14) are either indeterminate or appear much more like *M. dendroidea* than *M. transversa*. Unfortunately, d'Orbigny's type specimens (MNHN d'Orbigny Colln 6021) are missing from the tablet to which they were originally attached. The type locality is given as Grandpré, an Albian locality no longer available. *M. transversa* has not been recorded at this stratigraphical level elsewhere.

Family **incertae sedis**

Genus '***BERENICEA***' Lamouroux, 1821

Following Taylor & Sequieros (1982), the generic designation '*Berenicea*' is used informally for species of bereniciform tubuloporines in which the gynozooecium is unknown (*Berenicea* Lamouroux, 1821 is a *nomen dubium*). Reassignment of at least some of these species is anticipated after discovery of their gynozooecia.

'Berenicea' filifera Canu & Bassler, 1926 Fig. 102

1926 *Berenicea filifera* Canu & Bassler : 11; pl. 29, figs 3–4.

HOLOTYPE. USNM 69848, figd by Canu & Bassler (1926: pl. 29, figs 3–4).

DESCRIPTION. The zoarium is thin and unilamellar, bereniciform, with an irregular outline.

Autozooecial apertures are of moderate size, circular or slightly longitudinally elongate, very widely spaced in irregular quincunx, with thick, slightly raised peristomes up to 0·3 mm high where preserved in a hollow. Frontal walls are immersed.

MEASUREMENTS (from Canu & Bassler 1926). TAM, 0·12–0·13 mm; TPM, 0·17 mm; FWW, 0·24–0·30 mm.

REMARKS. The only available specimen of this rare species is the holotype which encrusts a sponge. The species resembles '*Berenicea*' *faringdonensis* but has more widely spaced apertures.

Canu & Bassler (1926: 11) describe the frontal walls as 'ornamented with small salient interrupted longitudinal *threads*'. Under the SEM these are seen to be the edges of the calcite crystals which form the recrystallized frontal walls.

'Berenicea' faringdonensis Canu & Bassler, 1926 Figs 103–104

1926 *Berenicea faringdonensis* Canu & Bassler: 11; pl. 29, figs 5–6.

HOLOTYPE. USNM 69847, figd by Canu & Bassler (1926: pl. 29, figs 5–6).

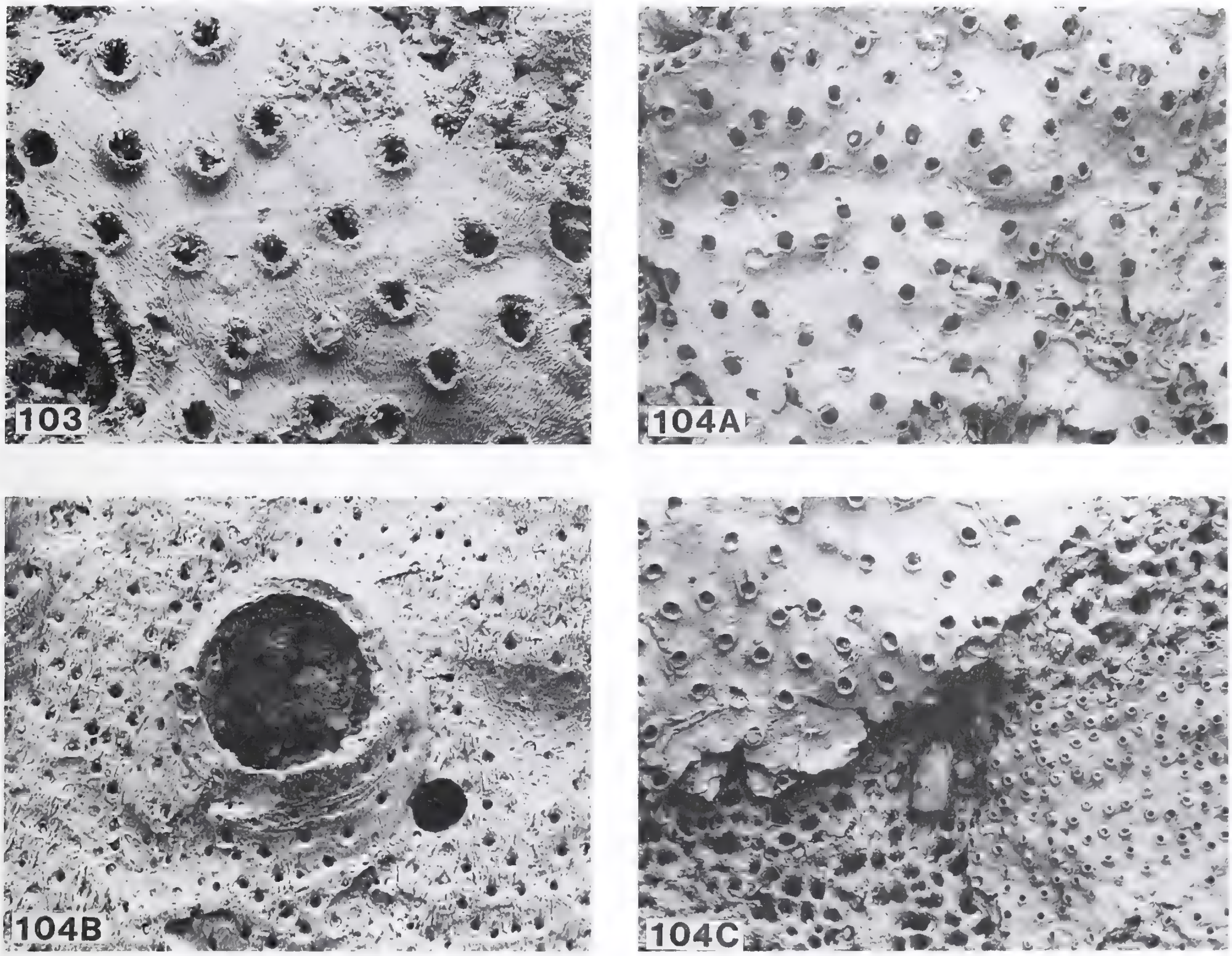
OTHER MATERIAL. BM(NH) D55070 Bowler's Pit, Pitt Colln; D55106 (with *Plagioecia orbifera* and Stomatoporid sp. 2), Little Coxwell Pit, Gaster Colln; D55125, Bowler's Pit, Gaster Colln; D55126, Little Coxwell Pit, Thomas Colln.

DESCRIPTION. Zoarium adnate, bereniciform and often large but thin. Intact growth margins have not been observed; the only available specimens are damaged remnants of large colonies.

Autozooecia are large and possess longitudinally elongate or circular apertures which are sometimes occluded by pseudoporous terminal diaphragms on top of short, distally-tapering peristomes. The zooecia are immersed, their slender frontal walls being only very gently convex, though zooecial boundaries may be marked by slight but conspicuous furrows. Pseudopores are circular.

Kenozooecia may be developed.

Indisputable gynozooecia are unknown. However, a single



Figs 103–104 *'Berenicea' faringdonensis* Canu & Bassler. Fig. 103, USNM 69847, holotype, × 25. Fig. 104, BM(NH) D55106; 104A, × 14; 104B, autozooecial aperture with small boring to the bottom right, × 150; 104C, colony encrusting a sponge and growing towards a colony of *Plagioecia orbifera* (Canu & Bassler), × 17.

doubtful gynozooecium observed in BM(NH) D55070 seems to have a *Hyporosopora*-like, transversely elongated frontal wall.

MEASUREMENTS. LAM, 0·15–0·17 mm; TAM, 0·14–0·15 mm; FWL, 0·84–1·20 mm; FWW, 0·21–0·24 mm.

REMARKS. All available specimens encrust sponges (Fig. 104C). The relatively flat colony surface serves to distinguish this species from *'Berenicea' grandipora* which has similarly large zooecia.

Specimen BM(NH) D55106 is bored by numerous small (*c*. 0·04 mm) holes which are arranged without regular pattern but usually restricted to one per zooecium (Fig. 104B). It is tempting to speculate that these were made by a predator.

'Berenicea' grandipora Canu & Bassler, 1926

Figs 105–106

1926 *Berenicea grandipora* Canu & Bassler: 11; pl. 28, figs 2–3.

HOLOTYPE. USNM 69846, figd by Canu & Bassler (1926: pl. 28, figs 2–3).

OTHER MATERIAL. BM(NH) D55069, D55071, Little Coxwell Pit, Gaster Colln.

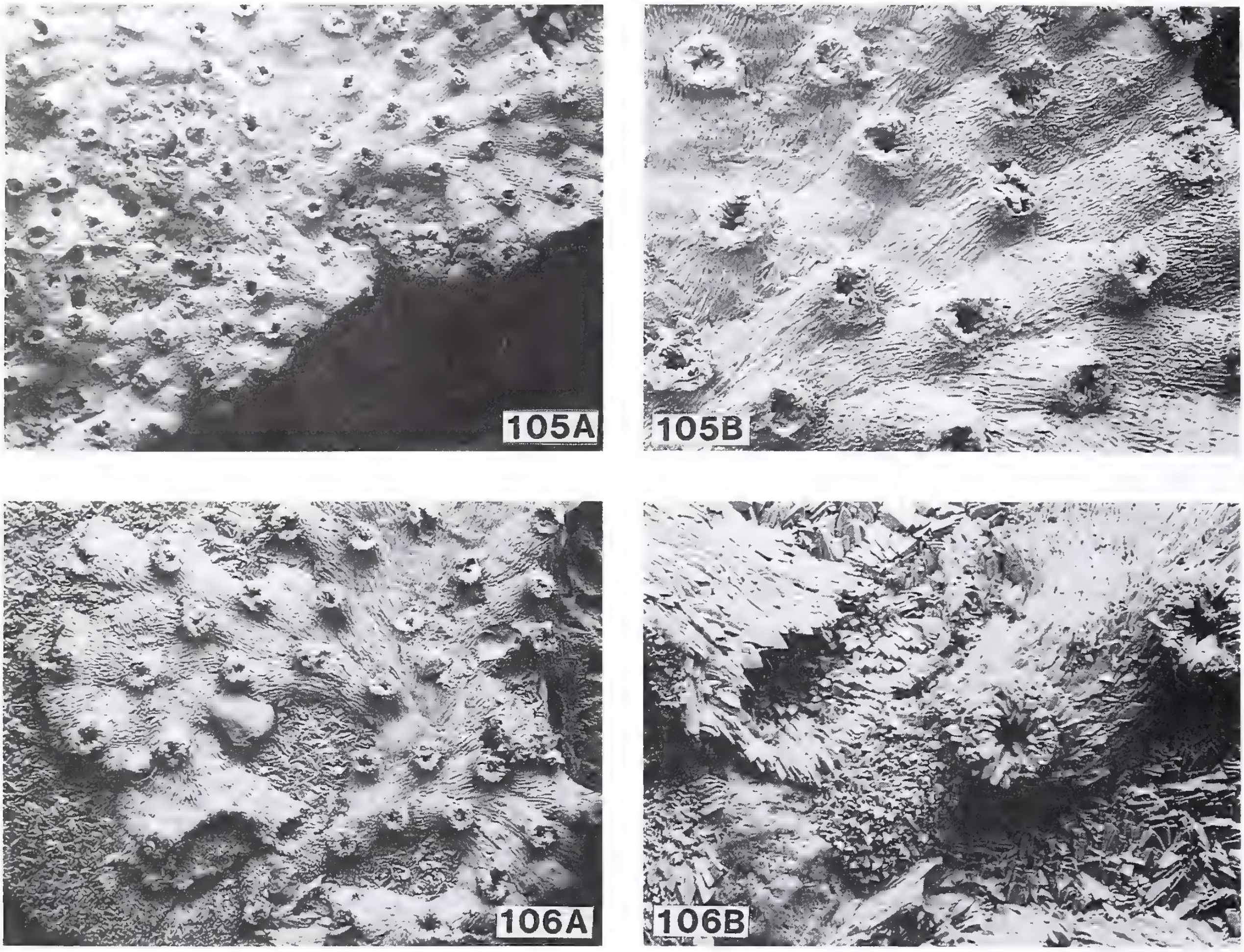
DESCRIPTION. Zoarium adnate, irregular in outline, typically fan-shaped bereniciform (Figs 105A, 106A), and thin, with only one generation of zooecial buds visible at the growth margin.

Autozooecia are large with convex frontal walls visible throughout their length (Fig. 105B). Maximum frontal wall width is often attained mid-length, giving the zooecia a flask shape. Apertures are large, though appreciably smaller than the maximum width of the frontal wall, circular or slightly transversely elliptical, and lacking significant preserved peristomes. Possible terminal diaphragms have been observed in the poorly-preserved holotype.

The ancestrula (Fig. 106B) is short (length inclusive of the protoecium 0·54 mm), and has a relatively narrow protoecium and a large aperture (*c*. 0·14 mm).

A possible partially-formed gynozooecium is present at the growing edge of BM(NH) D55069 (Fig. 106A), but is too incomplete to furnish useful information.

MEASUREMENTS. LAM, 0·17–0·20 mm; TAM, 0·15–0·18 mm; FWL, 0·90–1·19 mm; FWW, 0·27–0·35 mm.



Figs 105–106 *'Berenicea' grandipora* Canu & Bassler. Fig. 105, USNM 69846, holotype; 105A, × 8; 105B, autozooecia, × 30. Fig. 106, BM(NH) D55069; 106A, small, lobate colony, × 16; 106B, poorly-preserved ancestrula, × 70.

REMARKS. Zooecial dimensions are very similar in *'B.' grandipora* and *'B.' faringdonensis*. Canu & Bassler (1926) differentiated these two species firstly by the respectively regular or irregular arrangement of the apertures, but this is not borne out by their figures or by the type specimens. However, Canu & Bassler's second differentiating character, the respectively visible and immersed zooecia, provides a valid distinction. *'B.' grandipora* also differs from *'B.' faringdonensis* in the flask-shaped zooecia, the tendency for the autozooecial apertures to be transversely rather

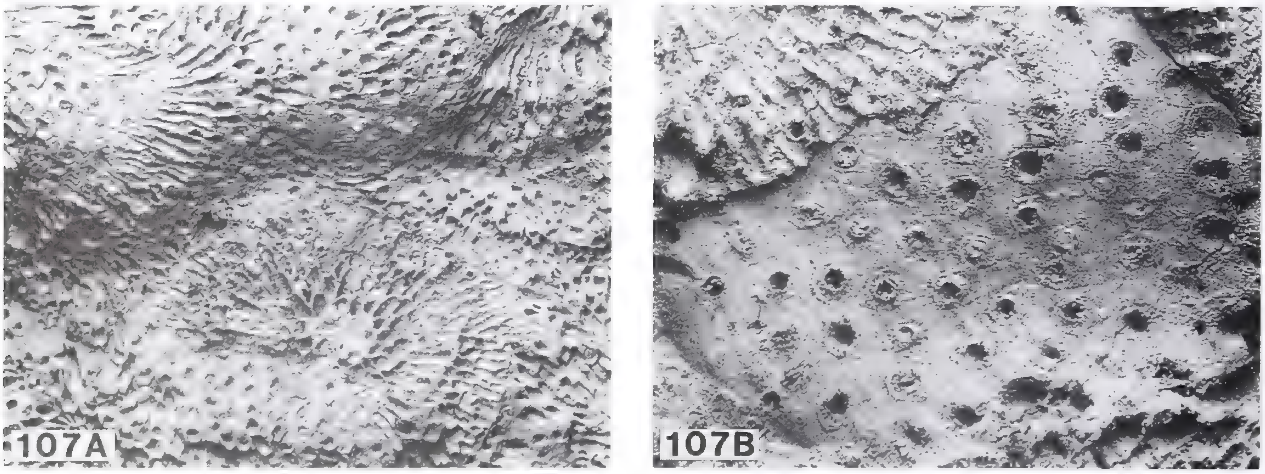
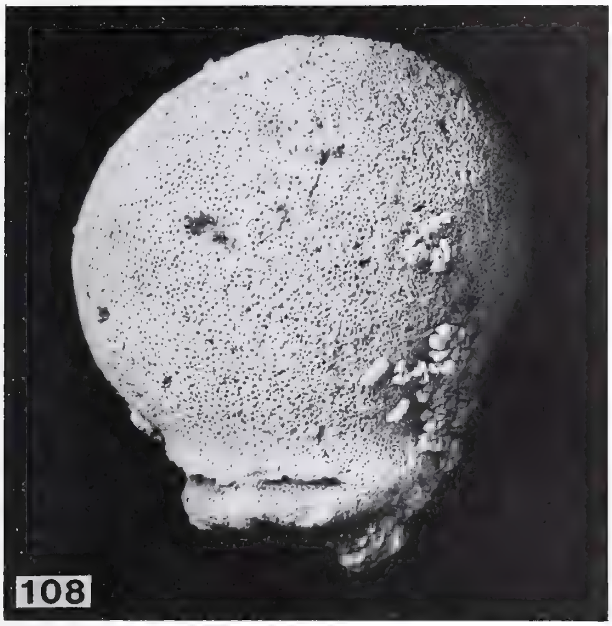


Fig. 107 *'Berenicea'* cf. *sowerbyi* (Lonsdale), BM(NH) D55347; 107A, abraded subcolonies, × 11; 107B, autozooecia (distal is to the left), × 28.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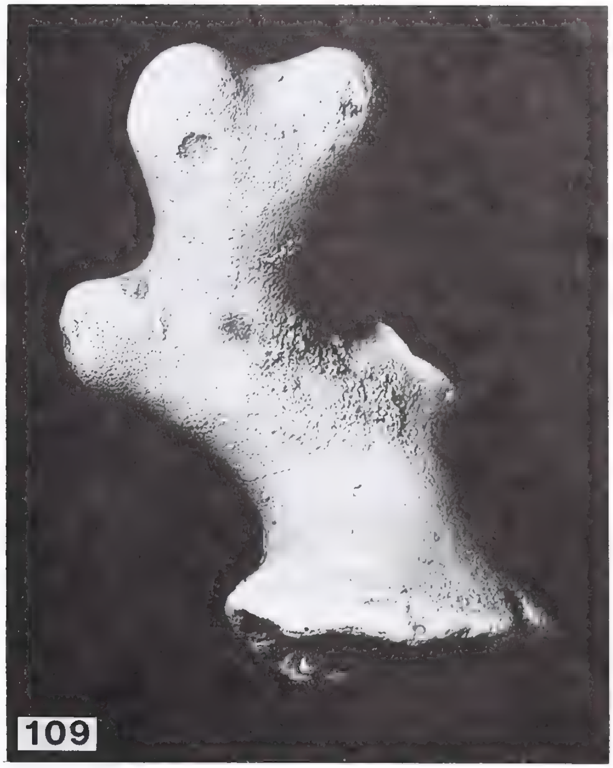
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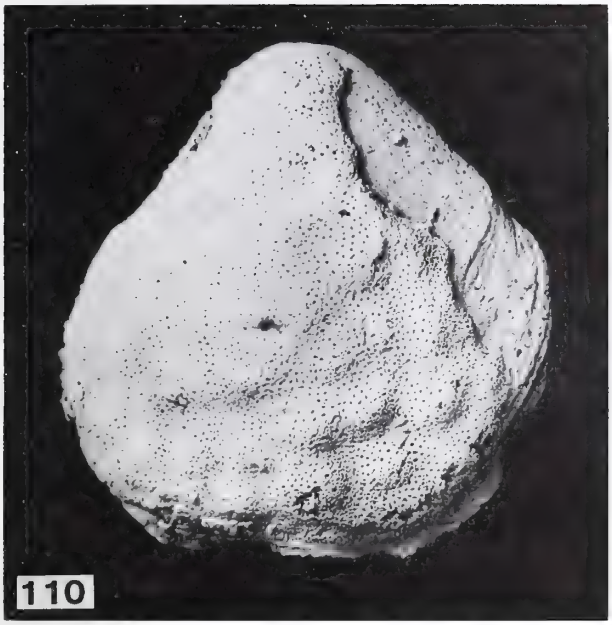
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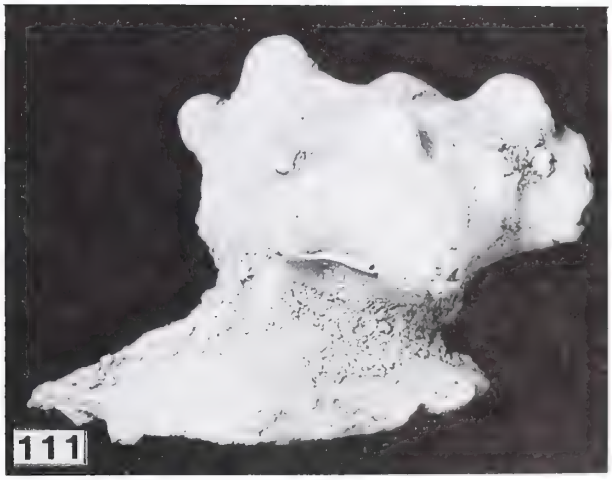
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Figs 108–111 Optical photographs of some cerioporine species. Fig. 108, *Heteropora clavata*, *sensu* Gregory (?*non* Kade), BM(NH) D55208, × 5·5. Fig. 109, *Heteropora keepingi* Gregory, BM(NH) D7169, × 2·8. Fig. 110, *Seminodicrescis variolata* (Gregory), BM(NH) D55299, colony encrusting a brachiopod, × 4·4. Fig. 111, *Ceriopora farringdonensis* Gregory, BM(NH) D7290, × 2·3.

than longitudinally elongate, and the lobate form of the colonies.

'Berenicea' cf. ***sowerbyi*** (Lonsdale, *in* Dixon 1850)

Fig. 107

?1971 *Reptomultisparsa* sp.; Hillmer: 46; pl. 3, fig. 7.

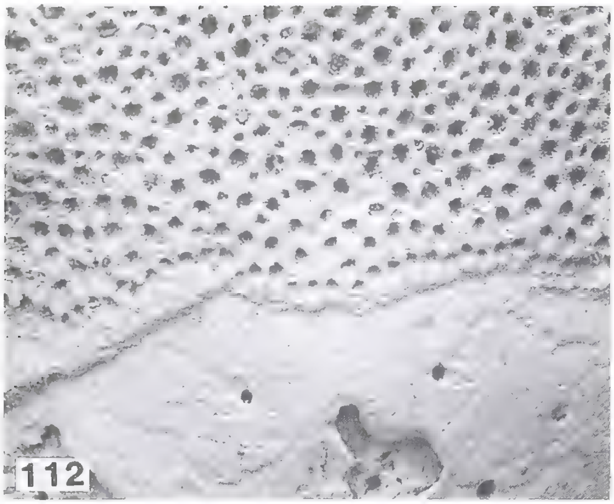
MATERIAL. BM(NH) D55347, Bowler's Pit, Gaster Colln.

DESCRIPTION. Colony encrusting, multilamellar, composed of numerous subcolonies arranged in a *Cellulipora*-like configuration. The subcolonies are subcircular in outline (Fig. 107B) and variable in size but often 5–6 mm in diameter. Only one tier of zooecial buds is normally visible at the growth margins of the thin subcolonies. New subcolonies appear to originate by eruptive frontal budding from the centres of established subcolonies.

Autozooecia (Fig. 107B) have well-defined frontal walls which taper proximally and are well-rounded distally. Apertures are circular, and preserved peristomes are thin and low.

MEASUREMENTS. TAM, 0·09–0·10 mm; TPM, 0·12–0·16 mm; FWL, 0·40–0·60 mm; FWW, 0·18–0·22 mm.

REMARKS. Although the solitary available specimen, which encrusts a sponge, is mostly worn, the better-preserved parts resemble an Upper Cretaceous specimen (BM(NH) D2991)



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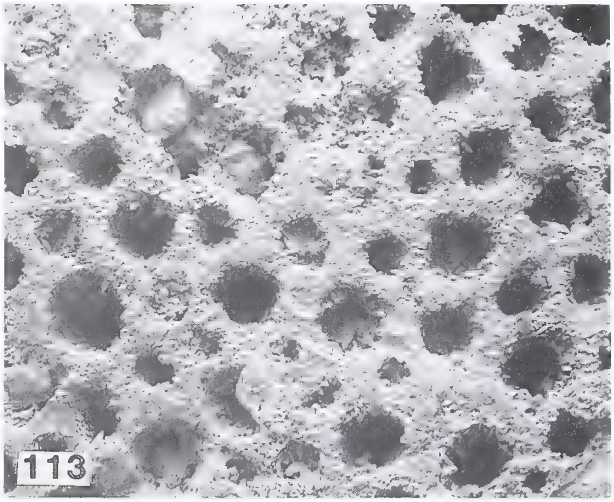

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Figs 112–113 *Heteropora clavata, sensu* Gregory (?*non* Kade). Fig. 112, BM(NH) D41378, overgrowth, × 30. Fig. 113, BM(NH) D55209, autozooecia and kenozooecia, × 95.

described as *Reptomultisparsa sowerbyi* (Lonsdale) by Gregory (1899). However, the zooecial dimensions of this Chalk bryozoan are smaller than in the Faringdon specimen. Lonsdale's (*in* Dixon 1850) type of *Diastopora sowerbyi* is unfortunately missing. The Faringdon specimen also resembles a colony figured by Hillmer (1971) from the Hauterivian of Germany as *Reptomultisparsa* sp. on account of the multilamellar growth-form.

Suborder **CERIOPORINA** von Hagenow, 1851
Family **HETEROPORIDAE** Waters, 1880

Genus ***HETEROPORA*** Blainville, 1830

Type species. *Ceriopora cryptopora* Goldfuss, 1826, designated by Gregory (1896); Maastrichtian of Maastricht, Netherlands.

Remarks. Numerous Jurassic to Recent cerioporine species have been referred by various authors to Blainville's (1830) genus *Heteropora*. Most possess dendroid branching colonies and well-defined zooecial dimorphism with autozooecial apertures surrounded by smaller kenozooecial apertures. This concept of the genus is, however, erroneous. Nye (1976) studied specimens of the type species, *H. cryptopora* (Goldfuss) from the Maastrichtian, and found no evidence of zooecial dimorphism. Furthermore, instead of having dendroid branches with endozones and exozones, colonies are bulbous and constructed of a series of overgrowths.

The correct generic assignment of dendroid, dimorphic cerioporines previously referred to *Heteropora* remains unclear. For the one such species (*Heteropora keepingi* Gregory) from the Faringdon Sponge Gravel the genus name *Heteropora* is therefore used tentatively. However, a second Faringdon species, *H. clavata, sensu* Gregory 1909*b*, may be more closely related to the type species.

Range. In the broad taxonomic sense, Aalenian to Recent.

Heteropora clavata*, sensu* Gregory 1909*b*, ?*non* Kade, 1852. Figs 108, 112–113

?non 1852 *Heteropora clavata* Kade: 32.
1909*b* *Heteropora clavata* Kade; Gregory: 64.
1909*a* *Heteropora clavata* Kade; Gregory: 192; fig. 51.

Material. BM(NH) D7294 (2 pieces and 1 thin section), Caleb Evans Colln (figd Gregory 1909*a*: fig. 51); D41378–9, D55209, D55210 (3 thin sections only), D55220, Little Coxwell Pit, Thomas Colln; D52187 (3 pieces and one acetate peel, comprising two specimens), Little Coxwell Pit, Pitt Colln; D55208, Little Coxwell Pit, Gaster Colln; D57583, Cleevely Colln; D57584, Little Coxwell Pit, Ware Colln.

Description. Zoarium club-shaped or subspherical (Fig. 108) with a slightly expanded base, up to 22 mm high by 15 mm wide. Overgrowths may arise on the 'head' and grow down the 'stalk' of the zoarium (Fig. 112). Maculae are apparently absent.

Zooecia are weakly dimorphic, circular to subcircular autozooecial apertures being surrounded by smaller kenozooecial apertures (Fig. 113). Some of the autozooecial apertures are occluded by diaphragms situated a little proximal of the apertural rim. Mural spines have not been observed but available material is not well preserved.

In thin sections the zoarium can be seen to consist of a succession of capping overgrowths with poorly-defined endozones. Zooecial walls are thick in endozones and exozones, indistictly laminated, sometimes moniliform in the exozone. Diaphragms, slightly aborally convex, may occur at intervals slightly greater than the width of the zooecial tubes and are commonly situated at different levels in adjacent zooecia. A single brood-chamber has been seen in section; it is covered by zooecia from the same overgrowth, and is 1·2 mm wide by 0·3 mm high, has an uneven floor of occluded zooecia, and a smooth roof supported by a few zooecia or septa, or both, which pass through the chamber.

Measurements. TAM, 0·08–0·10 mm; KAM, 0·03–0·06 mm.

Remarks. Kade's species *Heteropora clavata*, based on a drift specimen of uncertain age, was not figured in his original publication and cannot be recognized with certainty from the description. Professor E. Voigt (personal communication 1984) expressed doubt that the Faringdon species was conspecific with Kade's species. Gregory (1909*a*) suggested that Kade's name should be ignored because it is a *nomen nudum*,

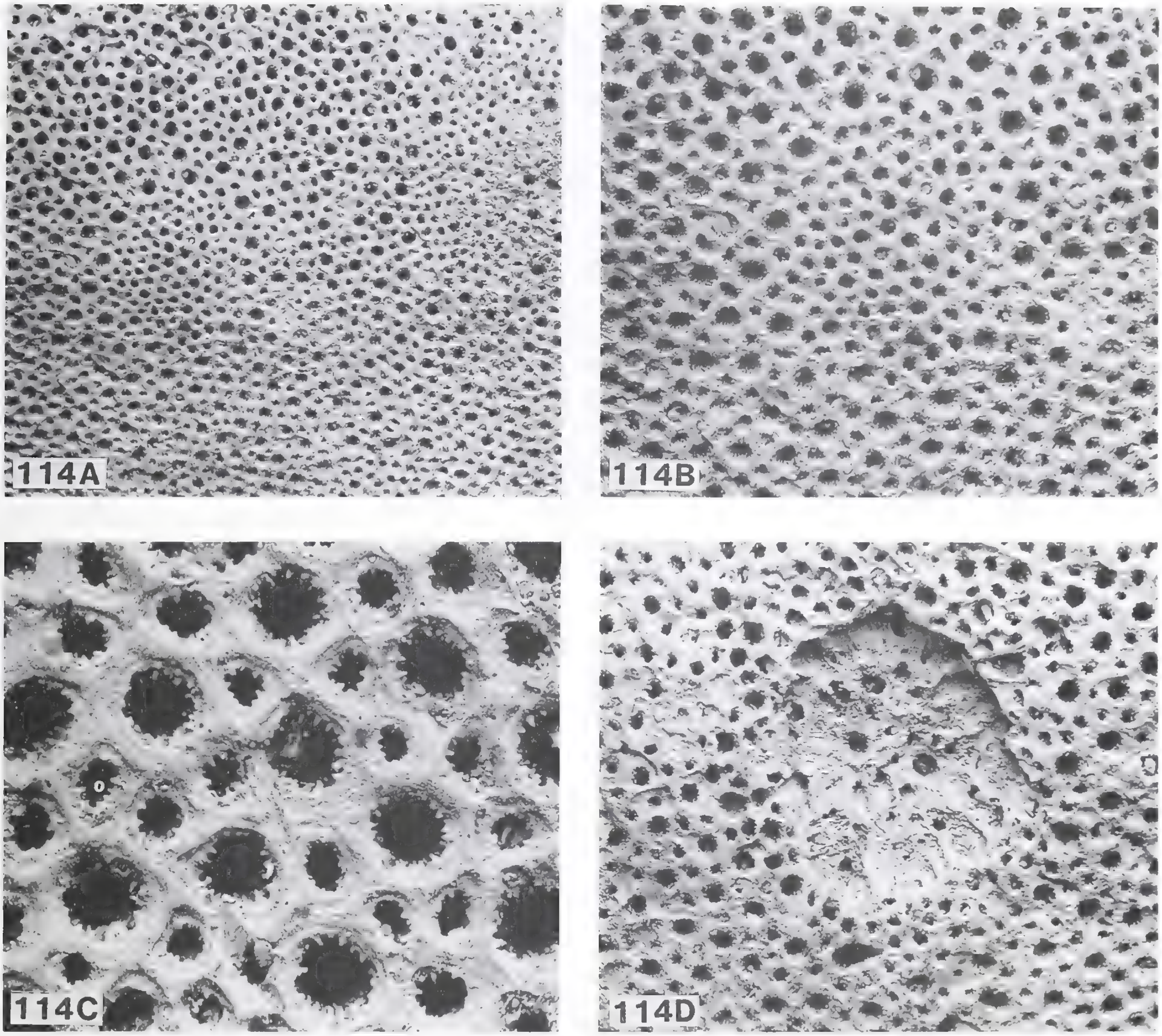

Fig. 114 *Heteropora keepingi* Gregory, BM(NH) D7292a, **lectotype** (herein selected); 114A, colony surface, × 21; 114B, maculum composed of kenozooecia, × 39; 114C, autozooecia and kenozooecia in intermacular area, × 130; 114D, worn brood chamber, × 38.

but went on to set up a Faringdon specimen, BM(NH) D7294, as the 'type' of the species. This specimen has no validity as the type of *H. clavata*; even if Kade's original material was shown to be lost, the Faringdon specimen cannot serve as a neotype because it comes from a widely different locality. Therefore, the correct name for the Faringdon species remains unclear, and it is herein referred to as *Heteropora clavata, sensu* Gregory, ?*non* Kade. We refrain from renaming it, pending more detailed study of better material.

This species can be distinguished from *H. keepingi* Gregory by the clavate colony-form, lack of maculae, apparent absence of mural spines and the multilayered structure of the colony, visible especially in thin sections.

Heteropora keepingi Gregory, 1909*b* Figs 109, 114–116

1909*b* *Heteropora keepingi* Gregory: 64.
1909*a* *Heteropora keepingi* Gregory; Gregory: 190; pl. 5, figs 7–8; fig. 50.
?1926 *Ceriopora dimorphocella* Canu & Bassler: 29; pl. 24, figs 1–6; pl. 31, figs 7–8; fig. 14.
?1926 *Heteropora nummularia* Canu & Bassler: 13; pl. 20, figs 6–8.

LECTOTYPE. BM(NH) D7292a, Faringdon, Cunnington Colln (figd Gregory, 1909*a*: pl. 5, fig. 7), is here chosen as lectotype.

PARALECTOTYPES. BM(NH) D7169 (of the four specimens mentioned by Gregory (1909*a*: 191) three remain), Faringdon, Ellis Colln; B118 (specimen and thin section), Lower Greensand, ?Isle of Wight (figd Gregory, 1909*a*: pl. 5, fig. 8; fig. 50).

OTHER MATERIAL. BM(NH) D7292b–c (these specimens were not listed by Gregory 1909*a* and, unlike D7292a, cannot be regarded as types), Cunnington Colln; D55215 (2 thin sections), D55216 (4 thin sections), D55218, D55219, Little Coxwell Pit, Thomas Colln; D55122, Little Coxwell Pit, Davis Colln. USNM 69872 (syntypes of *Ceriopora dimorphocella* comprising 1 thin section, 4 specimens and 3 remnants).

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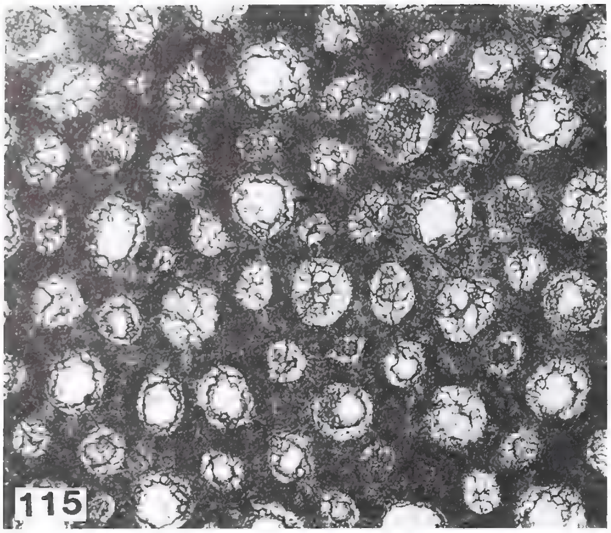

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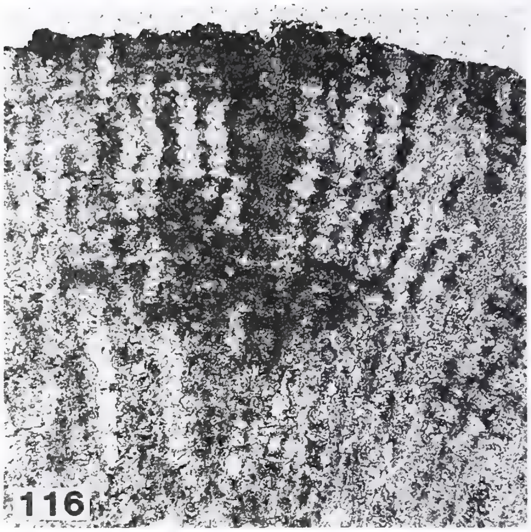


Figs 115–116 *Heteropora keepingi* Gregory, thin sections. Fig. 115, USNM 69872, syntype of *Ceriopora dimorphocella* Canu & Bassler, tangential section, × 74. Fig. 116, BM(NH) D55216, transverse section of exozone showing strongly moniliform zooecia, × 33.

DESCRIPTION. Zoaria (Fig. 109) are dendroid with thick branches, 8–15 mm in diameter, which bifurcate at intervals. Distal branch growth tips are blunt and rounded. Maculae, marked by concentrations of kenozooecia (Fig. 114B), are spaced about 3–4 mm apart on the zoarial surface. Zoarial bases are expanded but not extensive.

Autozooecial apertures are subcircular to polygonal, small, and surrounded by smaller, more angular kenozooecial apertures (Fig. 114C). Mural spines may be visible within both autozooecial and kenozooecial apertures; they are densely concentrated, taper distally, have rounded ends and are up to about 0·01 mm long.

Brood chambers (Fig. 114D) are visible as shallow depressions, approximately 2 mm in diameter, on the colony surface in the positions of maculae. Intact roofs have not been observed in hand specimens. Most of the autozooecia and kenozooecia below the chamber are occluded by a calcified layer forming the floor of the chamber.

Thin sections show the coaxial endozone (5 mm in diameter in D55216) and exozone, with moderately thick zooecial walls in the endozone and thick, distinctly moniliform walls in the exozone (Fig. 116). Diaphragms are absent or rare, and have aborally convex diaphragms. Brood chambers have not been observed in section.

MEASUREMENTS. TAM, mean 0·10 mm; KAM, mean 0·04 mm.

REMARKS. *Heteropora nummularia* Canu & Bassler, 1926, described from Faringdon, is represented by a single, worn specimen (USNM 69853). This is a flat, discoidal colony sharing with *H. keepingi* a similar arrangement of autozooecial and kenozooecial apertures which are, however, generally smaller in *H. nummularia* though variable in size. *H. nummularia* may be the early encrusting stage of *H. keepingi* before development of erect branches. *Ceriopora dimorphocella* Canu & Bassler (Fig. 115) seems also to be a junior synonym of *H. keepingi*.

H. keepingi can be confused with *Ceriopora farringdonensis* Gregory (see below) which, although normally more massive, can on occasions have a similar dendroid colony-form. Externally the two species can be distinguished by the lack of well-developed zooecial dimorphism and maculae in *C. farringdonensis*. In thin section the exozonal walls of *H. keepingi* are more distinctly moniliform, endozonal walls are thicker, diaphragms are less common, and the zooecial tubes have a smaller diameter.

Genus ***CERIOPORA*** Goldfuss, 1826

TYPE SPECIES. *Ceriopora micropora* Goldfuss, 1826, by subsequent designation of Gregory (1896); U. Cretaceous, locality uncertain (see Nye 1976: 56).

REMARKS. The type species of *Ceriopora* has been revised by Nye (1976), who gives a history of the concept of the genus. The name is generally applied to heteroporid species with massive, globular or subramose colony-forms, and lacking clearly defined dimorphism of the zooecia. Differences between *Ceriopora, Reptonodicava* d'Orbigny (see Nye 1976: 139), and *Ripisoecia* Canu & Bassler (see Walter, 1970) seem slight and clarification of the relationships between these genera will demand detailed morphological investigations of a wide range of species.

RANGE. ?Aalenian to ?Pliocene.

Ceriopora farringdonensis Gregory, 1909*b* Figs 111, 117

1909*b* *Ceriopora farringdonensis* Gregory: 63.
1909*a* *Ceriopora farringdonensis* Gregory; Gregory: 161; pl. 5, figs 1–4; fig. 42.

HOLOTYPE. BM(NH) 10298 (specimen and 1 thin section), Mantell Colln, figd Gregory (1909*a*: pl. 5, figs 1-2). No specimens are mentioned by number in the original description of this species (Gregory 1909*b*), but this specimen is stated as the type in the later paper by Gregory (1909*a*).

OTHER MATERIAL. BM(NH) 10237, 10302, Mantell Colln; D3144 (uncut specimen, thin section and 2 remnants; thin section figd Gregory 1909*a*: fig. 42), Brown Colln; D7290

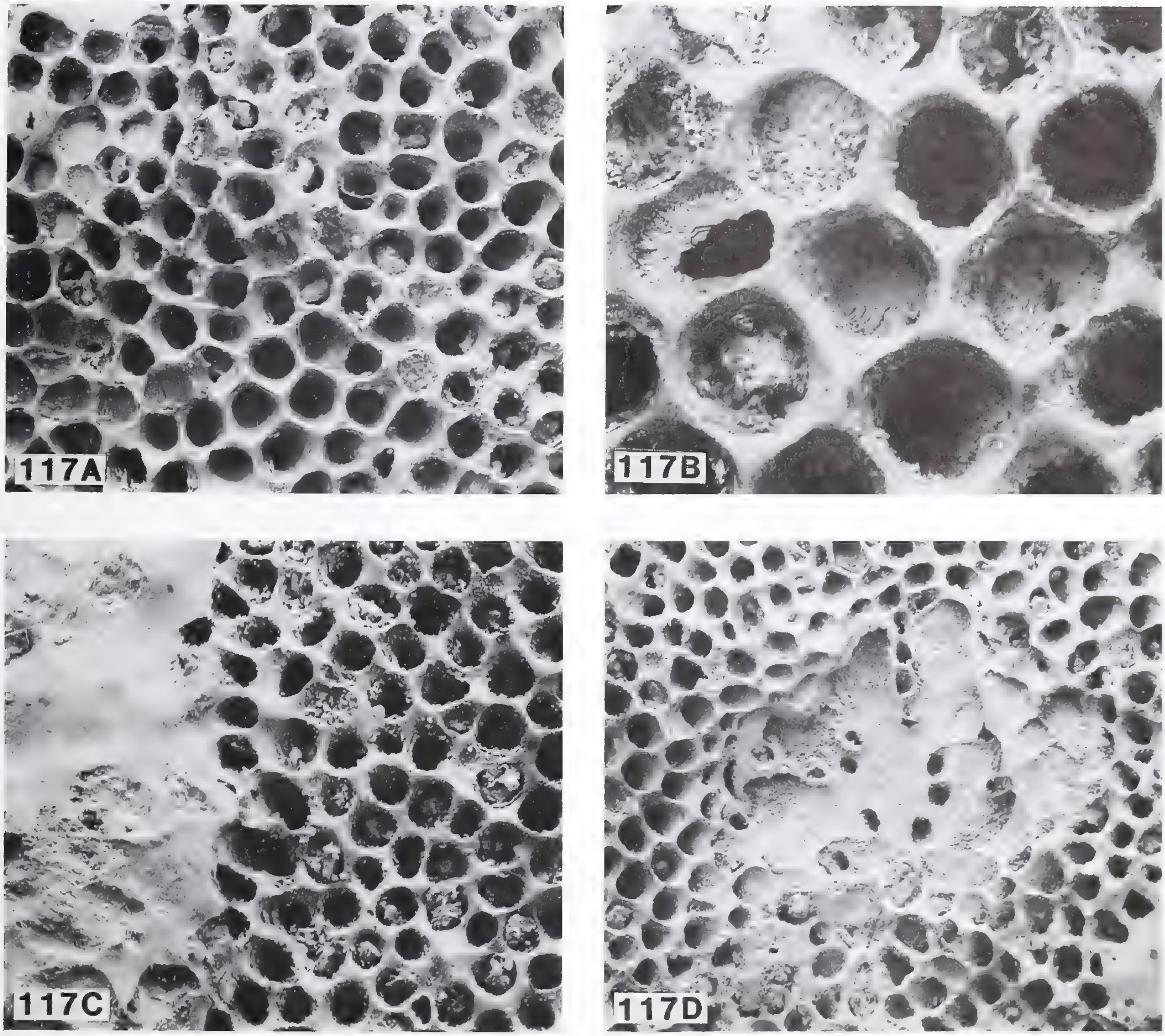


Fig. 117 *Ceriopora farringdonensis* Gregory, BM(NH) 10298, holotype; 117A, × 48; 117B, autozooecia, some with diaphragms, × 148; 117C, edge of overgrowth, × 36; 117D, incomplete brood chamber, × 32.

(reregistered from 55111; figd Gregory 1909*a*: pl. 5, fig. 3), Cunnington Colln; D7291 (figd Gregory 1909*a*: pl. 5, fig. 4), Sharp Colln; D37735, Ellis Colln (one of four specimens mentioned by Gregory (1909*a*: 191) as *Heteropora keepingi*, and re-registered from D7169); D57587, Little Coxwell Pit, Whiteley Colln; D57588–9 and D57590 (3 thin sections), Little Coxwell Pit, Pitt Colln; D57585, Little Coxwell Pit, Wise Colln; D57586, Wright Colln; D57591–2, Little Coxwell Pit, Davis Colln.

DESCRIPTION. Zoarium of variable form: massive, pedunculate with tuberous lobes (Fig. 111) or dendroid; massive zoaria are up to 50 mm across, branches of dendroid zoaria up to 27 mm in diameter. Overgrowths are commonly developed; the calcareous laminae (Fig. 117C) which occlude apertures over parts of colony surfaces appear related to intrazoarial overgrowths. Maculae are not generally visible although irregularly arranged monticule-like elevations may occur (Fig. 117A).

Zooecial apertures are monomorphic but very variable in size, and are subcircular to polygonal in shape. Diaphragms may occur a little beneath the level of the colony surface (Fig. 117B).

Brood chambers are preserved as depressions, 2–3 mm across, on the surface of zoaria. Autozooecia, linked by septum-like radial walls, apparently pierce brood chambers (Fig. 117D). Complete roofs have not been observed in hand specimen, and the ooeciopore is consequently unknown.

In section, branches of dendroid zoaria have thin-walled endozones and coaxial exozones. Zooecial walls in the exozone are moniliform and have an apparently granular microstructure with occasional dark patches. Brood chambers are seen to have thin, pseudoporous roofs, and their chambers (up to 3 mm wide by 0·5 mm high) are crossed by occasional zooecia and septa-like walls. Subterminal diaphragms commonly occur in zooecia beneath brood chambers and are situated a little proximally of the floor of the brood chamber.

MEASUREMENTS. TAM, 0·07–0·13 mm.

REMARKS. Although this species is fairly common at Faringdon and there are good specimens in most collections, Canu & Bassler (1926) apparently had no specimens and did not mention it. The distinction between *C. farringdonensis* and *H. keepingi* is discussed above (p. 118).

Genus *TETROCYCLOECIA* Canu, 1917

TYPE SPECIES. *Tetrocycloecia dichotoma* Canu, 1917, = *Ceriopora dichotoma* Goldfuss 1827, *sensu* Reuss, 1848, by original designation; Miocene, Eisenstadt, Austria.

REMARKS. The emendation of the genus name *Tetrocycloecia* to *Tretocycloecia* by Canu & Bassler (1920) has been followed by most subsequent authors, but Nye (1976) gives reasons for regarding this as unjustified, and the original spelling is used here.

Tillier (1975) and Nye (1976) have revised the type species of this genus, which in external morphology is very similar to *T. multiporosa* described below from Faringdon. However, *T. multiporosa* has kenozooecial apertures which are more funnel-shaped than in *T. dichotoma*. Furthermore, the clearly-differentiated ooeciopore is far smaller than the autozooecial apertures in *T. multiporosa*, whereas it is indistinct and may be the same size as an autozooecial aperture in *T. dichotoma*. Further detailed study is necessary to resolve whether the two species are really congeneric.

T. multiporosa may also be related to *Sparsicavea* d'Orbigny, 1853 (type species *S. carantina* d'Orbigny from the Turonian). Gynozooecial morphology, and autozooecial and kenozooecial arrangement are similar, although the walls of the kenozooecia tend to be raised into prominent surficial ridges in *Sparsicavea*.

RANGE. Aptian to Miocene.

Tetrocycloecia multiporosa Canu & Bassler, 1926

Figs 118–123

?1853 *Sparsicavea irregularis* d'Orbigny: 949; pl. 617, figs 5–7.

1926 *Tretocycloecia (?) multiporosa* Canu & Bassler: 83; pl. 16, figs 5–8.

1926 *Tretocycloecia densa* Canu & Bassler: 83; pl. 16, figs 9–14.

1926 *Sparsicavea irregularis* d'Orbigny; Canu & Bassler: 91; pl. 15, figs 11–14.

LECTOTYPE. USNM 69939b, figd Canu & Bassler (1926: pl. 16, fig. 5 (right-hand branch), and fig. 6), is here selected as the lectotype.

PARALECTOTYPES. USNM 69939a, figd Canu & Bassler (1926: pl. 16, fig. 5 (left-hand branch), and figs 7–8).

OTHER MATERIAL. BM(NH) D52158 (sample), D52224 (6), D52225 (sample), D55193 (sample), D55194 (2), D55196, D57718, Little Coxwell Pit, Pitt Colln; D55212, Bowler's Pit, Pitt Colln; D55195 (sample), D55206–7, D57717, Little Coxwell Pit, Gaster Colln; D55197 (2), Cleevely Colln; D57650 (10), Davis Colln; D55198 (2), Bowler's Pit, Thomas Colln; D55199, D55200 (6), D55201 (9), D55203, D55205 (2), D55213 (6), D55214 (sample), D57714–6 (thin sections), Little Coxwell Pit, Thomas Colln. USNM 69940 (4 syntypes of *T. densa* Canu & Bassler, 1926).

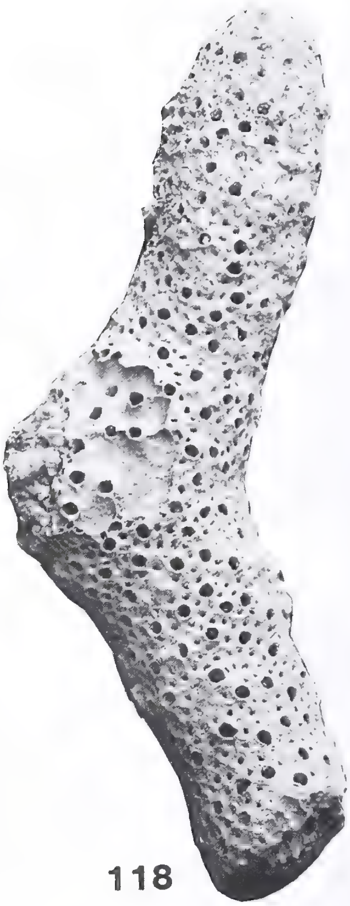


Fig. 118 *Tetrocycloecia multiporosa* Canu & Bassler, USNM 69939b, **lectotype** (herein selected), branch fragment with gynozooecium, × 23; see also Fig. 119.

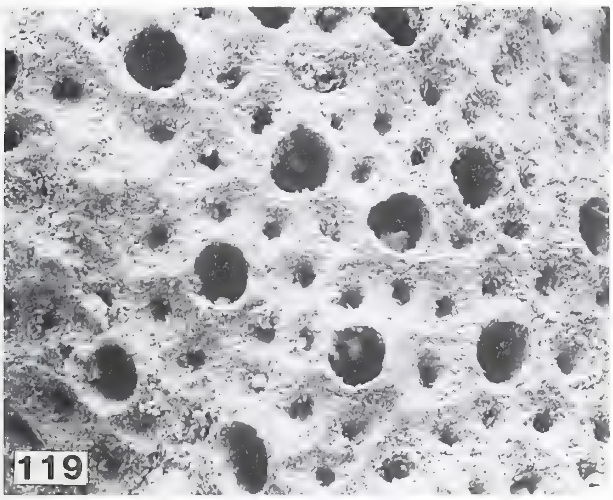
DESCRIPTION. Zoarium dendroid, vinculariiform (Fig. 118), with branches of moderate diameter (1–1·5 mm) which bifurcate and anastomose frequently. The colony base is a small conical expansion bearing a high concentration of kenozooecia.

Autozooecial apertures are small, circular, with a slightly protuberant rim, and are surrounded by kenozooecia (Fig. 119).

Kenozooecial apertures are very small, circular, funnel-shaped and depressed beneath the level of the colony surface, and polygonal in frontal outline.

Gynozooecia are common but are usually preserved with little or none of the frontal wall intact (Fig. 120). They are roughly circular in outline, and may be bulbous in relief, causing a localized swelling of the branch. The gynozooecial roof is a pseudoporous exterior wall which is penetrated by numerous autozooecia with thick apertural rims (Fig. 121A). Broken gynozooecia reveal that vertical internal walls as well as these autozooecia support the roof. The floor of the gynozooecium is formed of polygonal kenozooecial apertures occluded by a calcified lamina bearing very short mural spines; there may be a central funnel-like opening which is presumed to lead into the proximal part of the fertile zooecium. The rarely preserved ooeciopore (Fig. 121B) is situated in the centre of the gynozooecial roof, and is circular and very small, considerably smaller than an autozooecial aperture. The ooeciostome is slight.

In thin section, the endozone is seen to occupy about ⅔ of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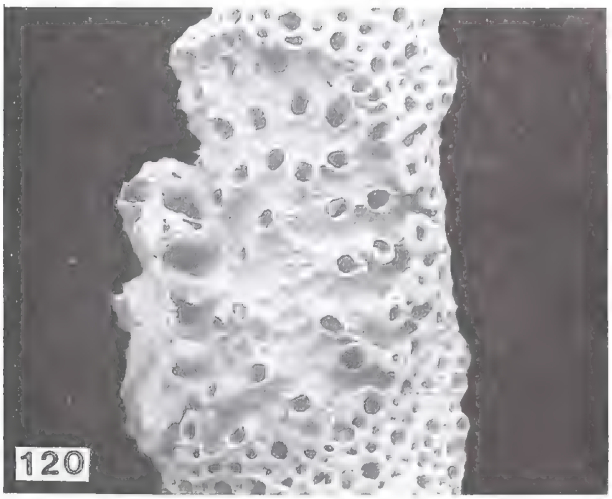
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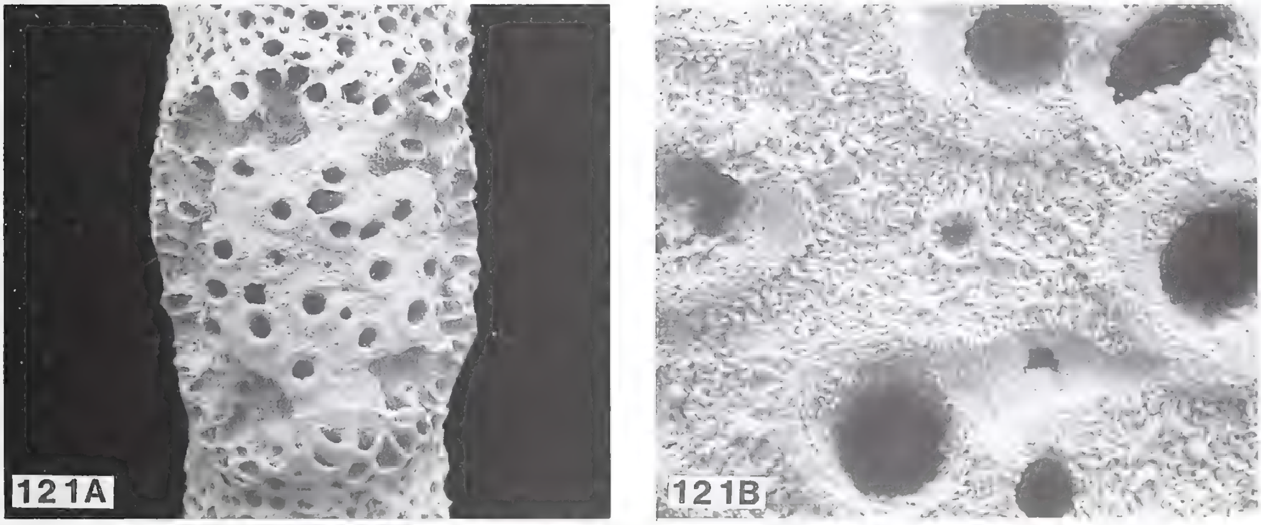
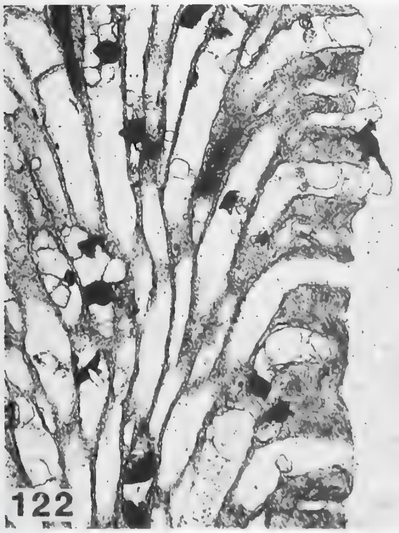

121A

121B

Figs 119–121 *Tetrocycloecia multiporosa* Canu & Bassler. Fig. 119, USNM 69939b, **lectotype**, autozooecia and kenozooecia, × 102; see also Fig. 118. Fig. 120, BM(NH) D57717, broken gynozooecium, × 30. Fig. 121, BM(NH) D55207; 121A, gynozooecium with relatively complete frontal wall, × 28; 121B, ooeciopore (centre), × 164.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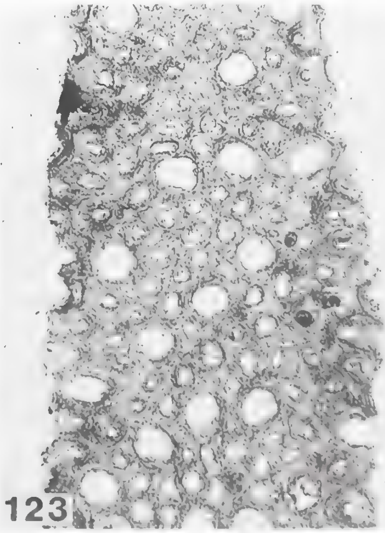
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Figs 122–123 *Tetrocycloecia multiporosa* Canu & Bassler, thin sections. Fig. 122, BM(NH) D57714, oblique longitudinal section, × 55. Fig. 123, BM(NH) D55715, shallow tangential section, × 55 the branch diameter, and is surrounded by an exozone in which zooecial walls thicken abruptly (Fig. 122). The kenozooecia appear to be budded around the endozonal–exozonal boundary. Zooecial walls are parallel-sided (i.e. not moniliform) and show well-developed rounded laminations in longitudinal section in the exozone. Some of the autozooecia are partitioned by thin diaphragms in the endozone. Most diaphragms are orally flexed where they meet the zooecial walls (basal diaphragms), but some near the outside of the endozone are aborally flexed.

MEASUREMENTS (ranges of mean values from four colonies, except for ooeciopore). TAM, 0·07–0·08 mm; TPM, 0·11–0·13 mm; KAM, 0·03–0·05 mm; width of kenozooecial frontal surface area, 0·10 mm; GDL, 0·60–2·00 mm; GW, 0·90–1·50 mm; LOPM, 0·03 mm; TOPM, 0·03 mm.

REMARKS. Canu & Bassler (1926) used three separate species names for material from Faringdon which is here described as *T. multiporosa*. One of these species, *Sparsicavea irregulare* d'Orbigny, originally described from the Albian of the Ardennes, is difficult to intëpret from d'Orbigny's figures and description, but may possibly be a senior synonym of *T. multiporosa. T. densa* Canu & Bassler was distinguished from *T. multiporosa* by the smaller size of the kenozooecia ('mesopores'). This difference is, however, gradational and seems related to the ontogenetic stage of the kenozooecia.

Genus *CLAUSA* d'Orbigny, 1853

TYPE SPECIES. *Ceriopora heteropora* d'Orbigny, 1850, by subsequent designation of Gregory, 1899; Cenomanian of France.

REMARKS. The vinculariiform branches of species of *Clausa* are characterized by the presence of numerous polygonal kenozooecia, sometimes occluded by terminal diaphragms, surrounding the circular, open apertures of the autozooecia. These kenozooecia have often been referred to as 'dactylethrae', and Gregory (1896) used their occurrence to define a cyclostome suborder, Dactylethrata, which was retained by Bassler (1953) in the 'Treatise'. However, dactylethrae as understood by Gregory (1896) comprise at least two non-homologous structures: occluded kenozooecia as in *Clausa*, and autozooecia occluded during late ontogeny as in *Terebellaria*. There appears to be no sound basis for recognizing the Dactylethrata, some genera of which are apparently tubuloporines (e.g. *Reticulipora, Terebellaria*) and others cerioporines (e.g. *Clausa, Reptomulticlausa*).

Although gynozooecia have been described in the type species of *Clausa*, none have been found in the Faringdon species *Clausa zonifera*. In *C. heteropora*, gynozooecia have a strongly digitate outline (Walter *et al.* 1975) and appear to be roofed with exterior wall. Together with the absence of calcified exterior frontal walls in the autozooecia, this implies classification of *Clausa* with the cerioporines as currently understood. There is a good resemblance in external morphology between *Clausa* and some Recent heteroporids (e.g. *Heteropora pelliculata*, see Borg 1933: pl. 3, fig. 4) in which occluded kenozooecia surround circular autozooecial apertures. Therefore, *Clausa* is here assigned to the Heteroporidae with the caveat that more research is required, particularly on internal morphology.

RANGE. Aptian to ?Recent. Extension of the range of *Clausa* from the Cretaceous into the Recent rests on the synonymy (Brood 1972), which requires confirmation, of the living genus *Bientalophora* Borg, 1944 with *Clausa*.

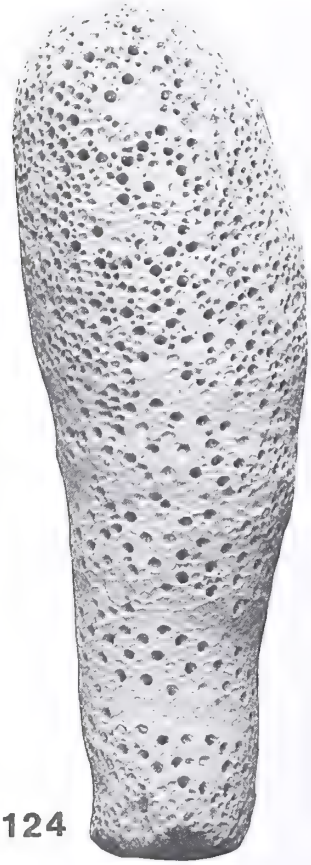
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Fig. 124 *Clausa zonifera* Canu & Bassler, USNM 69935d, **lectotype** (herein selected), × 14.

Clausa zonifera Canu & Bassler, 1926 Figs 124–127

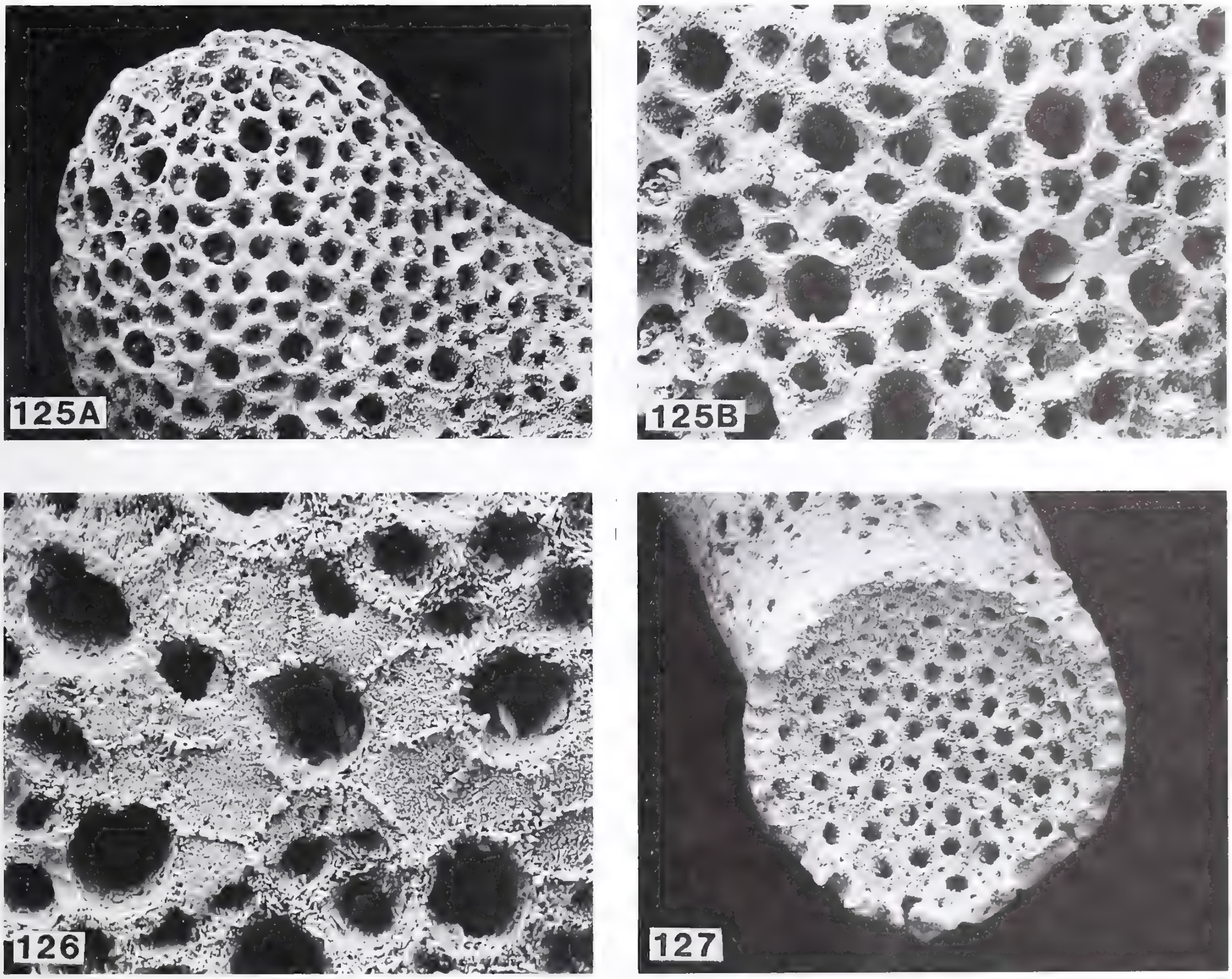
1926 *Clausa zonifera* Canu & Bassler: 80; pl. 17, figs 8–11; pl. 31, fig. 9.

LECTOTYPE. USNM 69935d, figd by Canu & Bassler (1926: pl. 17, figs 10–11), is here chosen as the lectotype.

PARALECTOTYPES. USNM 69935a-c, e-g, and one thin section.

OTHER MATERIAL. BM(NH) D52148 (sample), D52183 (sample), D55087–9, D57729 (3 thin sections and remnant), D57735, Little Coxwell Pit, Pitt Colln; D52129–39 (sample), D52150 (6), D52153 (sample), D57719–20, Little Coxwell Pit, Thomas Colln; D52148 (sample), D55149 (2), Little Coxwell Pit, Gaster Colln; D55151 (sample), D55152 (2), Bowler's Pit, Gaster Colln; D55154 (sample), Bowler's Pit, ?colln; D57651 (5), Davis Colln.

DESCRIPTION. Zoaria erect, dendroid, with cylindrical branches (averaging 2·5 mm diameter, range 1·5–3 mm) which are often claviform and swollen (Fig. 124). Branch growth tips are blunt and well-rounded (Fig. 125A). Branches bifurcate at irregular intervals and at angles up to 90°. The colony base is small, slightly expanded and has a high density of kenozooecia. More than one erect stem may arise from each colony base, and early bifurcations may be closely spaced. The proximal fractured ends of branches are



Figs 125–127 *Clausa zonifera* Canu & Bassler. Fig. 125, BM(NH) D57719; 125A, growth tip, × 52; 125B, autozooecia and open kenozooecia, × 100. Fig. 126, BM(NH) D57720, autozooecia and occluded kenozooecia, × 138. Fig. 127, BM(NH) D57735, concave proximal fracture surface of a branch, × 35.

sometimes concave (Fig. 127), breakage apparently occurring at a position of weakness, possibly a growth check. Ill-defined maculae are usually developed and consist of bands, aligned transverse to growth direction, which are rich in kenozooecia.

Autozooecia have open, circular apertures, lack frontal walls, and are surrounded by kenozooecia (Figs 125B, 126).

Kenozooecia have smaller, more variably-sized apertures than autozooecia. Occlusion of kenozooecial apertures is common (Fig. 126); occluded apertures appear polygonal whereas open apertures appear rounded. Terminal diaphragms are apparently pseudoporous and are situated slightly below the level of the aperture so that the interzooecial walls stand out as low ridges.

Brood chambers are unknown.

In section, zooecial walls are indistinctly laminated and relatively thick in the endozone. Diaphragms other than terminal diaphragms have not been observed. Kenozooecia are seen to bud in the exozone which is poorly differentiated from the endozone.

Measurements. TAM, 0·10–0·14 mm; KAM, 0·02–0·09 mm.

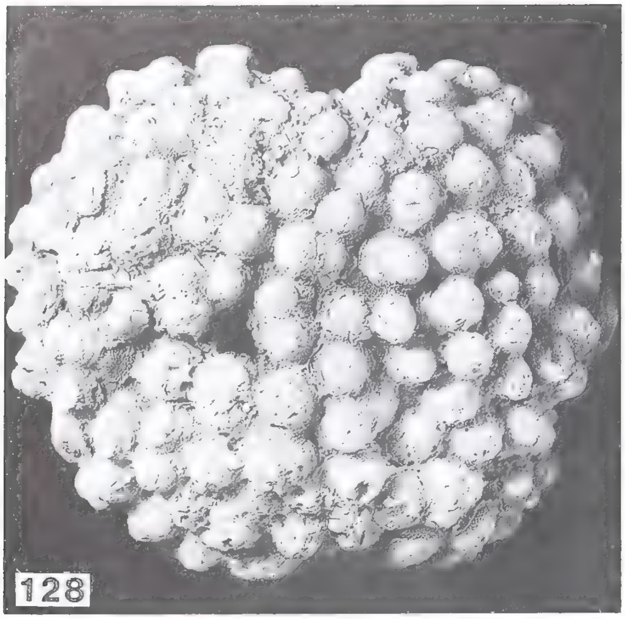
Remarks. This species is very common at Faringdon but has not been recorded elsewhere. It is most likely to be confused with *Tetrocycloecia multiporosa* which shares with *Clausa zonifera* a similar arrangement of autozooecia and kenozooecia in the dendroid colony branches. However, there are several points of distinction including: the larger size of colony branches and autozooecial apertures in *C. zonifera*; the slight autozooecial peristomes and typically funnel-shaped kenozooecia in *T. multiporosa*; and the occurrence of maculae, swollen branches, and kenozooecia occluded by terminal diaphragms in *C. zonifera*.

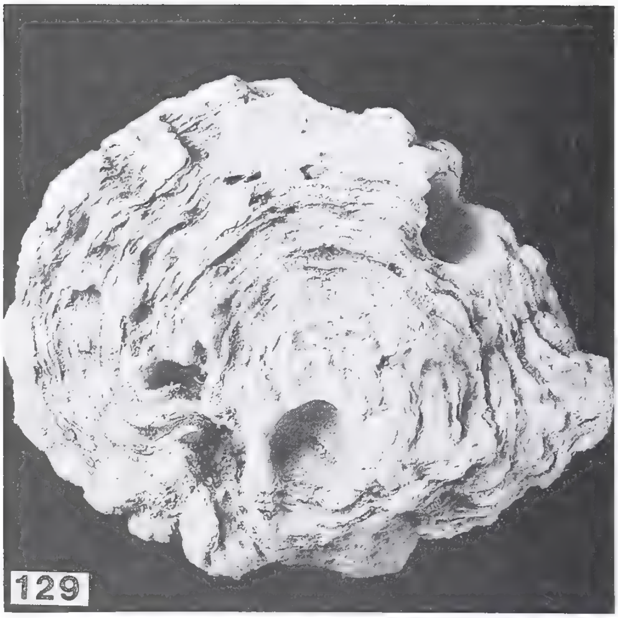
Family **incertae sedis**

Genus ***SEMIMULTICAVEA*** d'Orbigny, 1854

Type species. *Ceriopora landrioti* Michelin, 1841, by subsequent designation of Gregory, 1909*a*; Albian of Grandpré, France.

Remarks. Walter (1975) redescribed the type material of the type species of *Semimulticavea*. The multilamellar colony is constructed of stacked polygonal subcolonies with radially-arranged autozooecia separated by polymorphs (termed cancelli by Walter). Unfortunately, brood chambers are not





Figs 128–129 *Semimulticavea marginata* (Canu & Bassler), optical photographs. Fig. 128, BM(NH) D55117, mammilate colony surface with numerous subcolonies, × 2·1. Fig. 129, BM(NH) D55114, fractured colony with bivalve boring (*Gastrochaenolites*), × 1·8.

described and therefore the subordinal status of the genus is unclear. Brood chambers in *S. marginata* are, however, described below and imply that *Semimulticavea*, in spite of the presence of possible pseudolunaria (see Brood 1972: 71 for a definition of these structures), may be a cerioporine and not a rectangulate as previously considered (e.g. Bassler 1953).

RANGE. Aptian to ?Campanian.

Semimulticavea marginata (Canu & Bassler, 1926)

Figs 128–136

1909*a* *Radiopora neocomiensis* (d'Orbigny); Gregory: 284; text-figs 74–75.

1926 *Radiopora tuberculata* (d'Orbigny); Canu & Bassler: 63; pl. 20, figs 2–5.

1926 *Multigalea canui* (Gregory); Canu & Bassler: 61; pl. 19, figs 1–6 [non *Reptomulticava canui* Gregory 1909*b*].

1926 *Multigalea marginata* Canu & Bassler: 62; pl. 19, figs 7–10.

HOLOTYPE. USNM 69911, figd Canu & Bassler, 1926: pl. 19, figs 7–10.

OTHER MATERIAL. BM(NH) 10178, 10189, 10300, Mantell Colln; D3143 (with 3 remnants and 3 thin sections), figd as *Radiopora neocomiensis* (d'Orbigny) by Gregory (1909*a*); D4985, Brown Colln; D52203, D55365, D55367–8, Little Coxwell Pit, Pitt Colln; D55114, D55364, D55372, Bowler's Pit, Pitt Colln; D55113, Little Coxwell Pit, A.G. Davis Colln; D55117, D57722 (3 thin sections), Bowler's Pit, Gaster Colln; D55366, Little Coxwell Pit, Cleevely Colln; D55369, Little Coxwell Pit, Thomas Colln; D57723 (3 thin sections), Little Coxwell Pit, A. G. Davis Colln.

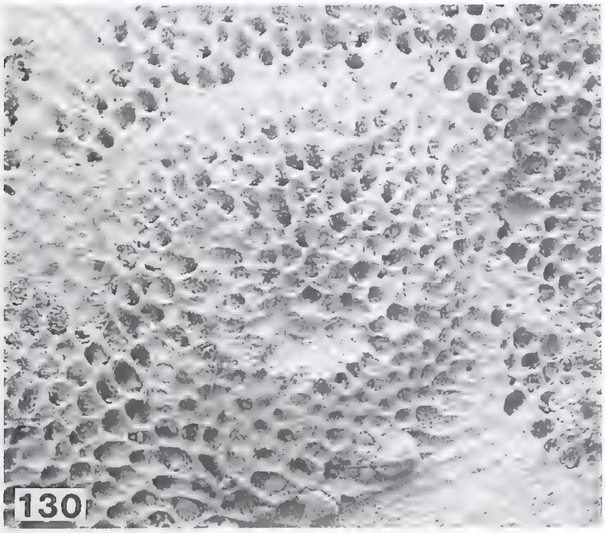
DESCRIPTION. Zoarium massive and multilamellar (Figs 128–129, 135), typically large (up to 70 mm across), usually irregularly hemisperical, but occasionally shaped like a carrot and up to 95 mm high with an axial hole (due to growth around an unpreserved substrate). In some places the successive layers are tightly packed, but elsewhere there may be significant amounts of void space between the layers (Fig. 132). Each layer consists of numerous low and broad, inverted cup-shaped subcolonies which are fused with adjacent subcolonies along part or all of their edges, and are subcircular to polygonal in plan view (Fig. 131B). The surface of the colony is monticulate, the monticule summits being the centres of the subcolonies. Each subcolony has an axial area of kenozooecia surrounded by radiating, uniserial rows, sometimes ill-defined, of autozooecia which are separated by kenozooecia (Fig. 131B); in worn specimens the distinction between autozooecia and kenozooecia is not appartent (Fig. 130). Subcolonies of successive layers are aligned directly above one another (Figs 132, 136A), reflecting the origin of new subcolonies from the centres of established subcolonies.

Autozooecial apertures are polygonal to subcircular and vary greatly in size, decreasing towards the centre of the subcolonies. In well-preserved specimens (e.g. in sheltered recesses) crescent-shaped ?pseudolunaria (Figs 131A, 134), up to 0·1 mm high, may occur on the sides of the apertures closest to the centres of the subcolonies.

Kenozooecia are located at the centres of subcolonies and between the rows of autozooecia, and have small subcircular apertures lacking ?pseudolunaria.

Gynozooecia (Fig. 133) are uncommon and in surface outline appear to be ring-shaped and centred on a subcolony, or possibly crescent-shaped. The frontal wall is a smooth-textured, probable exterior wall (though pseudopores have not been observed) and is pierced by autozooecia arranged in typical uniserial rows. All observed gynozooecia are broken and no unequivocal ooeciostomes have been identified.

In thin section the zooecial walls have a granular, cloudy microstructure without clearly visible laminations. Interzooecial walls are thin in the endozone and thick and moniliform (with interzooidal pores) in the exozone (Fig. 136B). A few zooecia have single, thin diaphragms of the



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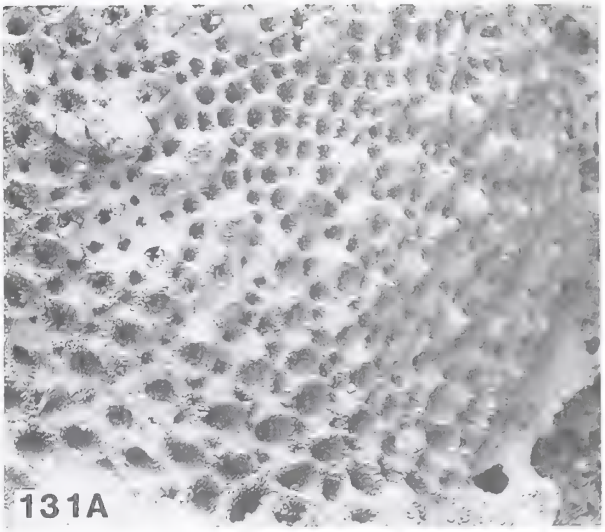
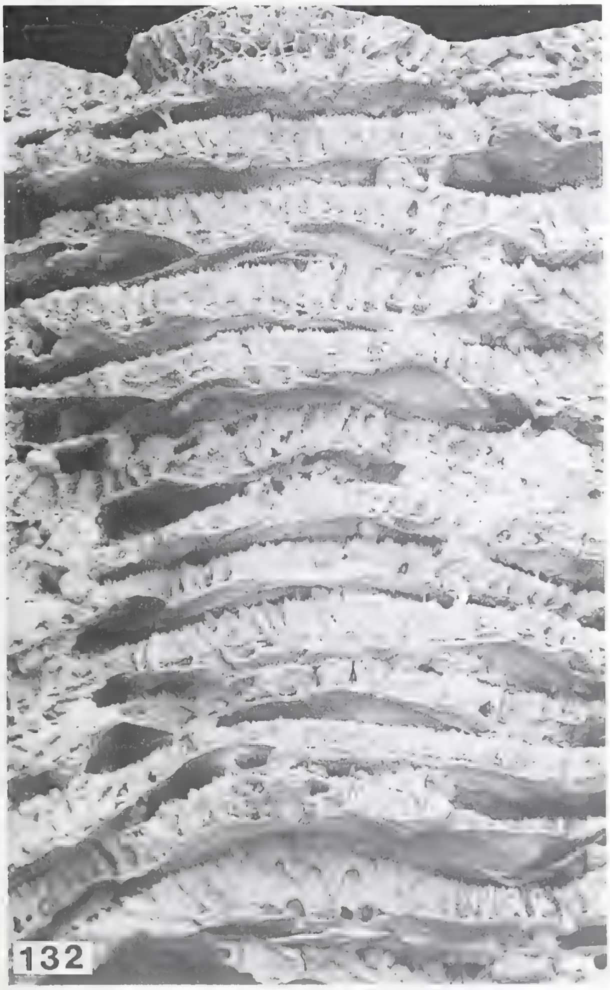


131A



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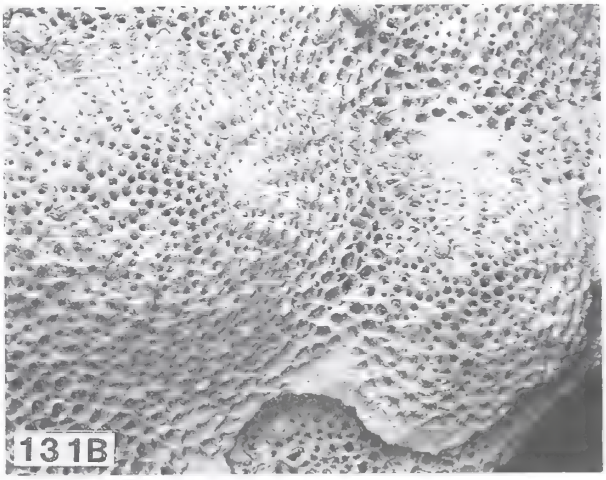
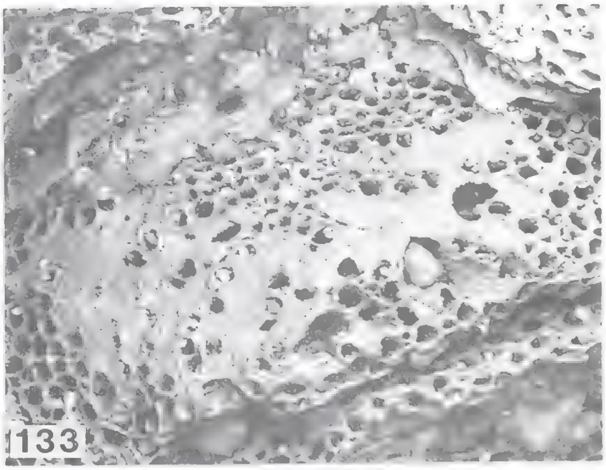


131B



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Figs 130–133 *Semimulticavea marginata* (Canu & Bassler). Fig. 130, USNM 69911, holotype, abraded subcolony, × 15. Fig. 131, BM(NH) D55113; 131A, autozooecia with ?pseudolunaria flanking a monticular subcolony, × 31; 131B, two subcolonies, × 10. Fig. 132, BM(NH) D55371, part of a fractured colony showing multilayered structure, × 15; see also Fig. 134. Fig. 133, BM(NH) D55368, gynozooecium, × 21.

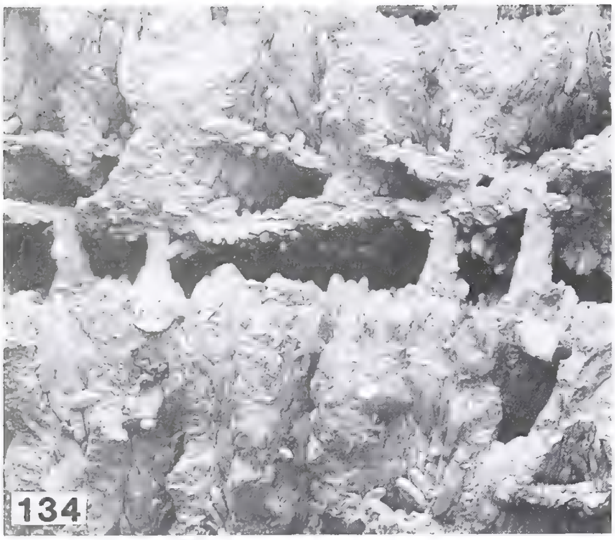


Fig. 134 *Semimulticavea marginata* (Canu & Bassler), BM(NH) D55371, part of a fractured colony showing four spine-like ?pseudolunaria covered by the next layer of colony growth, × 103; see also Fig. 132.

intermediate type which are flexed aborally at their contacts with the zooecial walls. Zooecial chambers near the centres of the subcolonies may be seen to continue into overlying subcolonies (Fig. 136B). The distinction between autozooecia and kenozooecia is not readily made in thin section.

MEASUREMENTS. TAM, 0·10–0·15 mm; KAM, 0·04–0·05 mm.

REMARKS. Specimens of this species from Faringdon have usually been referred to as *Radiopora neocomiensis* d'Orbigny. However, there are complex systematic problems resulting from the use of this name.

Firstly, *Radiopora* d'Orbigny, 1849 is an inappropriate genus for the Faringdon species. The type species, by original designation, is *Ceriopora formosa* Michelin from the Cenomanian of Le Mans, which has a ramose colony-form with stellate subcolonies. D'Orbigny (1854: 992–998) attributed 10 species to *Radiopora*, including *Radiopora formosa* (Michelin) from the type locality of Le Mans. D'Orbigny's illustrations of *R. formosa* are reproduced or redrawn from Michelin's original figures; the dendroid branches are almost certainly not multilayered and therefore unlike so-called *Radiopora* from the Faringdon Sponge Gravel.

The species *neocomiensis* was originally described in the binomen *Monticulipora neocomiensis* d'Orbigny (1850: 95) and characterized thus: 'Éspece tubereuse, à monticules très reguliers. Fontenoy, Chenay'. D'Orbigny later (1854: 993–994), placed his species in synonymy with *Alveolites heteropora* Roemer, 1836 [*sic*], as *Radiopora heteropora* d'Orb. 1852 [*sic*], and figured (1854: pl. 781, figs 13–16) a massive multilayered colony with monticules and radiating rows of autozooecial apertures. The species *heteropora* had been first described by Roemer (1839, not 1836) from the Neocomian of Germany in the binomen *Alveolites heteropora* (1839: 14; pl. 17, figs 7–8). Roemer's poor illustrations depict a small encrusting species with thick walls surrounding tiny apertures. This is clearly not the same as the species which was called *Radiopora heteropora* by d'Orbigny (1854).

A second genus to which the Faringdon species has been referred is *Multigalea*. This genus was proposed by Canu & Bassler (1926: 61), who designated *Reptomulticava canui* Gregory, 1909*b* as the type species. Unfortunately, the identity of *R. canui* is in doubt. *R. canui* was erected by Gregory as a 'nov. nom.' for *Reptomulticava tuberosa* (Roemer), *sensu* d'Orbigny (1854), which Gregory believed to differ from *Alveolites tuberosa* Roemer. In fact the species *R. canui* is not a new name but a new species. Gregory (1909*b*) did not figure *R. canui* in his original paper, and failed to do so also in his subsequent catalogue (1909*a*). Ascertaining the identity of *R. canui* is further complicated by Gregory's (1909*a*: 130) statement: 'The specimen figured by d'Orbigny [as *Reptomulticava tuberosa*], according to M. Pergens, is lost; accordingly the Museum specimen, D.7077, had better be regarded as type [of *R. canui*]'. This statement can be interpreted as an effective neotype designation; however, the specimen cited cannot serve as a neotype because it is from Goslar rather than one of the two type localities (St Dizier and Vassy, France) given by Gregory (1909*b*). Therefore, there is no valid type specimen for *R. canui* and, as Gregory's two descriptions (1909*b*,*a*) are inadequate to characterize the species, the identity of the genus *Multigalea* of which it is the type species cannot be ascertained at present.

After dismissing *Radiopora* and *Multigalea* as appropriate genera to accommodate the Faringdon species, *Semimulticavea* d'Orbigny remains as the most suitable generic assignment. The type species of *Semimulticavea* is *Ceriopora landrioti* Michelin, redescribed by Walter (1975), from the Albian of the Ardennes. Colonies of this species are multilamellar and are constructed of numerous subcolonies each with radial rows of autozooids separated by kenozooids.

In describing their new species *Multigalea marginata*, Canu & Bassler (1926) provided the correct specific name for the

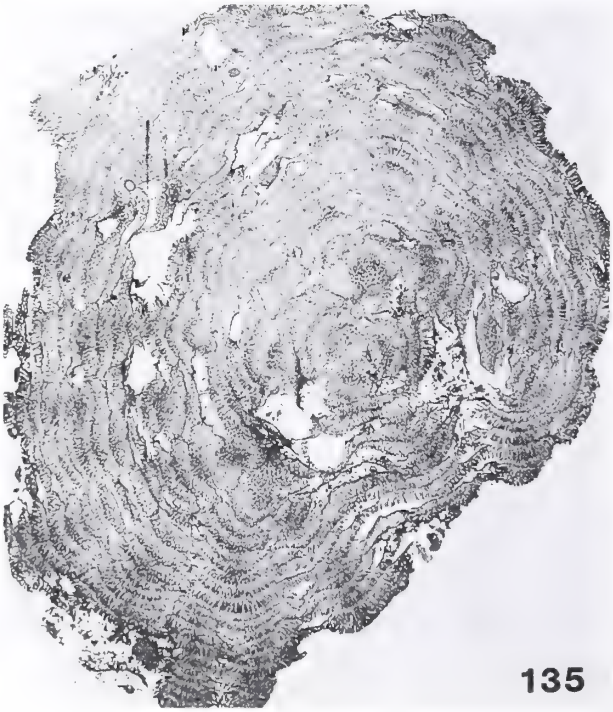


Fig. 135 *Semimulticavea marginata* (Canu & Bassler), BM(NH) D57722, thin section showing multilayered structure of colony, × 2·6; see also Fig. 136.

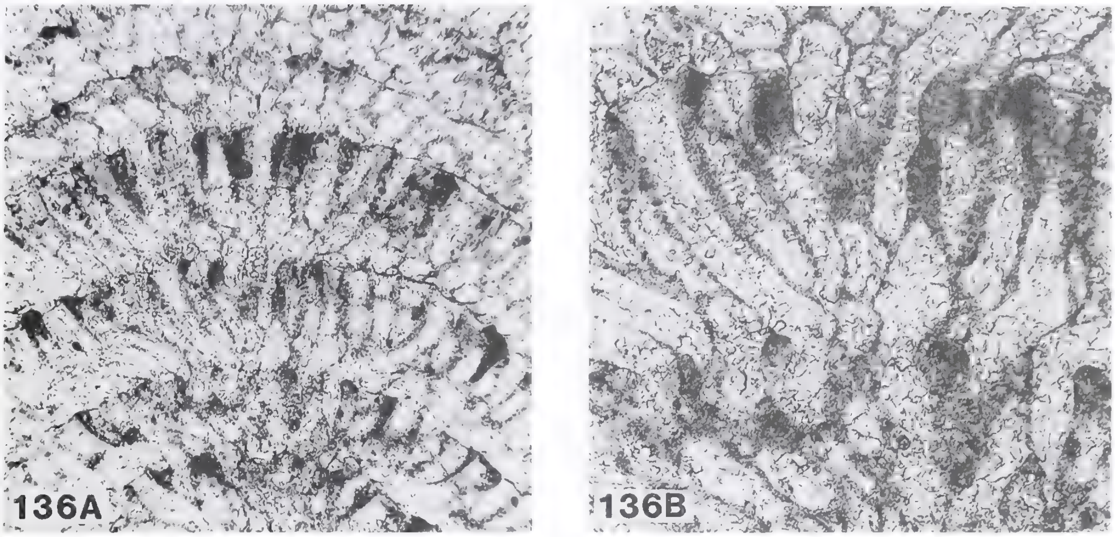


Fig. 136 *Semimulticavea marginata* (Canu & Bassler), BM(NH) D57722, thin section; 136A, vertical section through the origins of a stack of subcolonies, × 22; 136B, detail showing some zooecia continuing from parent to daughter subcolony, × 55; see also Fig. 135.

common Faringdon species. Unfortunately, the holotype of *S. marginata* (Canu & Bassler) is heavily worn (Fig. 130) and does not show the ?pseudolunaria of the autozooecia.

S. marginata bears a close resemblance to *Ceriopora (Reptonodicava) nodosa* Keeping, 1883, the syntypes (SM B26133–9) of which have been studied. Keeping's specimens of this species from the Aptian of Upware share with *S. marginata* large multilamellar colonies composed of numerous subcolonies. However, the subcolonies are larger and the monticules typically higher than in *S. marginata*. Furthermore, dimorphism of the zooecia is not clearly developed and pseudolunaria cannot be observed, though this may be because of the abraded state of the material.

Colonies of *S. marginata* are distinctive on account of their multilayered structure and typically large size. Probably the carrot-shaped colonies of *S. marginata* came from a pit closed long ago; none have been found in the last fifty years (carrot-shaped colonies also occur in *C. nodosa* Keeping, e.g. SM specimens B26137 and B29139). Hemispherical colonies are also much less commonly found nowadays than they were in the past.

Serpulid tubes are encountered embedded within colonies between successive layers. These worms evidently fouled the surfaces of living colonies and were subsequently trapped by the growth of new overarching subcolonies. Also commonly associated with *S. marginata* are boring bivalves whose crypts (ichnogenus *Gastrochaenolites*) are found penetrating many colonies (Fig. 129).

Genus ***SEMINODICRESCIS*** d'Orbigny, 1854

TYPE SPECIES. *Seminodicrescis nodosa* d'Orbigny, 1854, by monotypy; Aptian of Saint-Dizier (Haute-Marne) and Croutes (Aube), France.

REMARKS. *Seminodicrescis* was founded by d'Orbigny (1854) for a heteroporid-like Aptian species, *S. nodosa*, with a hollow tubular colony-form. Unfortunately, the type material of *S. nodosa* has yet to be revised, and the detailed morphology of the genus is not apparent from d'Orbigny's description and figures. However, the Faringdon species *Semimulticavea variolata* of Gregory (1909*a*), which may occur as hollow tubular colonies or as conventional encrusting colonies on shells, etc., sufficiently resembles the type species of *Seminodicrescis* for provisional assignment to this genus.

RANGE. Aptian.

Seminodicrescis variolata (Gregory, 1909*a*)

Figs 110, 137–139

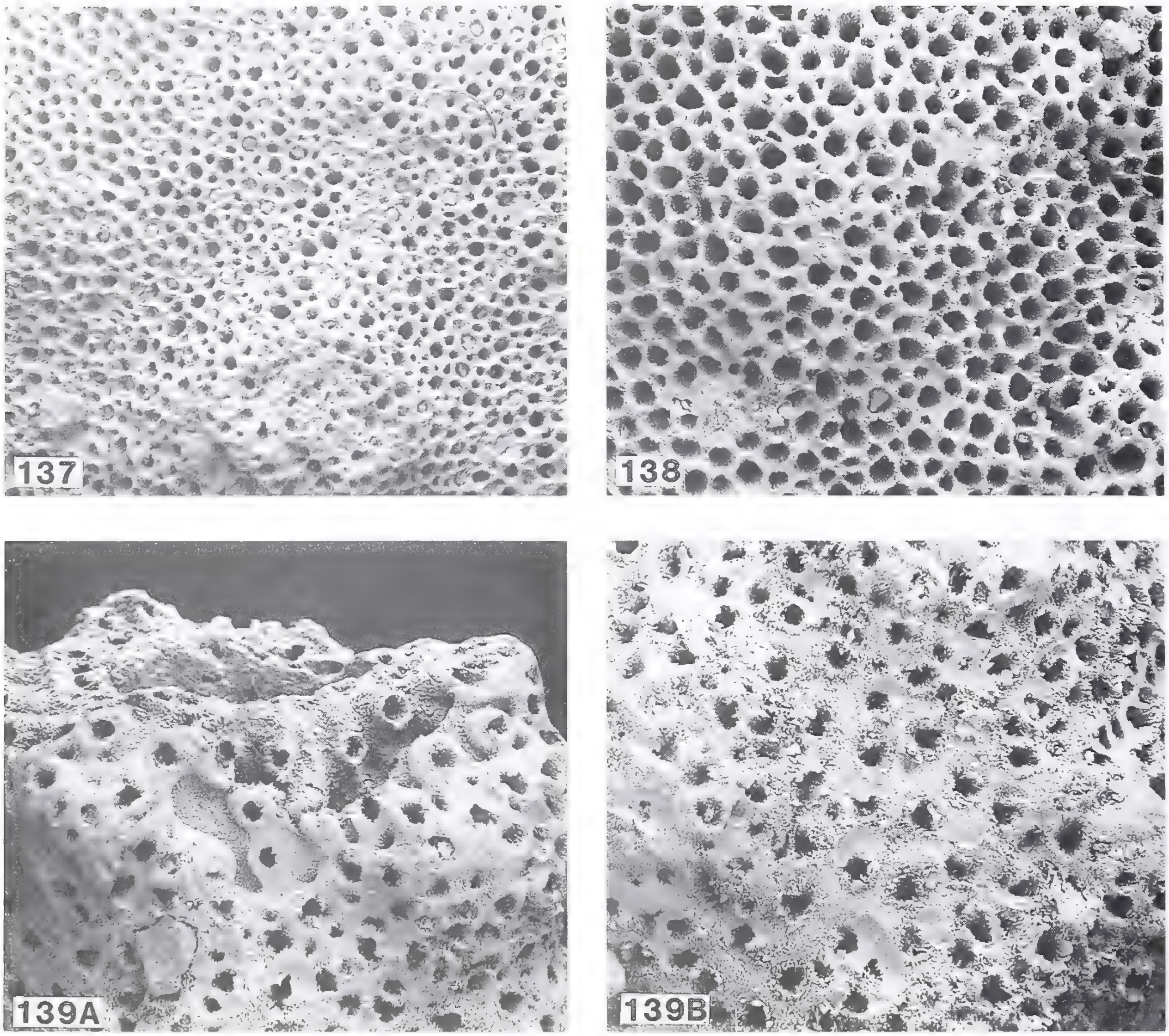
1909*a* *Semimulticavea variolata* Gregory: 241; pl. 5, figs 5a, c.
1926 *Multicrescis mammillosa* Canu & Bassler: 16; pl. 21, figs 5–6 [pl. 21 includes two figures labelled 6; that in the centre of the plate may not be this species].
1926 *Seminodicrescis nodosa* d'Orbigny; Canu & Bassler: 19; pl. 22, fig. 1.
1986 *Multicrescis mammillosa* Canu & Bassler; Wilson: 694.

HOLOTYPE. BM(NH) D3027.

OTHER MATERIAL. BM(NH) D52169 (sample), Little Coxwell Pit, Pitt Colln; D52296 (sample), D55300, D57721 (sample), Little Coxwell Pit, Thomas Colln; D55295, Hinde Colln; D55297 (3), locality presumed to be Faringdon, *ex* Durham University Colln; D55298–9, D55203–5, Little Coxwell Pit, Gaster Colln; D55427, Wicklesham Pit, Wilson Colln. USNM 69860, type specimen of *Multicrescis mammillosa* Canu & Bassler, 1926.

DESCRIPTION. Zoarium encrusting (Fig. 110, p. 115), sometimes tubular, usually unilamellar but occasionally multilamellar, with moderately to well developed monticules (Fig. 138) which may possess smaller kenozooecia than the intermonticular areas. The observation of zooecia apparently giving rise to new buds by intrazooecial fission suggests that this process may have been responsible for multilamellar overgrowth.

Autozooecial apertures are small, polygonal to subcircular,



Figs 137–139 *Seminodicrescis variolata* (Gregory). Fig. 137, USNM 69860, type specimen of *Multicrescis mammilosa* Canu & Bassler, × 15. Fig. 138, BM(NH) D55297a, monticule, × 36. Fig. 139, BM(NH) D52169a; 139A, broken gynozooecium, × 48; 139B, gynozooecium with poorly-preserved but intact frontal wall, × 52.

and may have slight peristomes which help distinguish them from kenozooecia.

Kenozooecial apertures are smaller and more angular than the autozooecia which they surround.

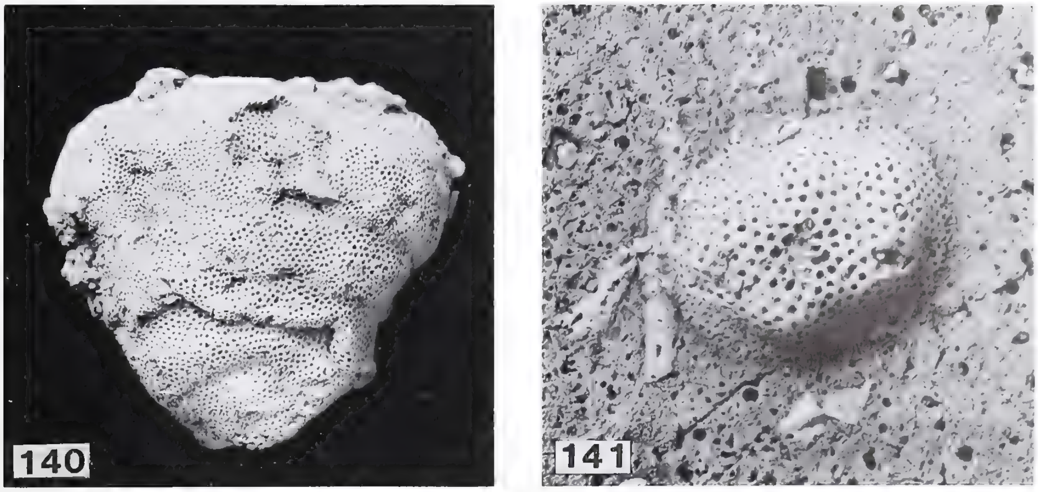
Brood chambers (?gynozooecia) are rare (Fig. 139). They are more-or-less circular in outline, about 1·2 mm in diameter, and are roofed by a probable exterior wall which is penetrated by numerous autozooecia. In addition to these penetrating autozooecia, the roof is supported by septa-like internal walls. The ooeciopore has not been observed.

MEASUREMENTS. TAM, 0·07–0·10 mm, mean 0·08 mm; KAM, 0·03–0·06 mm, mean 0·05 mm.

REMARKS. This species is distinguished from *S. nodosa* d'Orbigny by the considerably smaller size of the autozooecia; Walter *et al.* (1975) give the diameter of the autozooecial apertures in *S. nodosa* as 0·15–0·16 mm, whereas those of *S. variolata* are 0·07–0·10 mm.

The oldest available name for this species derives from Gregory (1909*a*) who provided a short description based on a single specimen. In their description of the Faringdon bryozoan fauna, Canu & Bassler (1926) appear to have overlooked Gregory's species and proposed *Multicrescis mammillosa* for their material. They also used the name *Seminodicrescis nodosa* d'Orbigny for hollow tube colonies of *S. variolata* which apparently encrusted perishable cylindrical substrates.

S. variolata is especially common encrusting small terebratulid brachiopods, usually on the pedicle valve (Fig. 110). On articulated specimens the bryozoan colony often extends to the edge of the pedicle valve but does not cross the commissure. One such colony (BM(NH) D55297) is penetrated by a paraboloid boring which passes through both bryozoan and brachiopod shell and may be the hole made by a predator of the brachiopod. If so, some colonies of *S. variolata* may have been symbionts of living brachiopods (i.e. true epizoans). However, other colonies of *S. variolata* are tubular and encrust vinculariiform bryozoans, erect serpulid worm tubes,



Figs 140–141 *Reptomulticava brydonei* (Gregory), optical photographs. Fig. 140, BM(NH) D77753, × 4·2. Fig. 141, BM(NH) D55325, young colony encrusting a bivalve shell, × 11·5.

echinoid spines or soft-bodied substrates. Small shell fragments were also occasionally used but the species has not been found among the diverse encrusting bryozoan fauna developed on sponges or pebbles.

Genus ***REPTOMULTICAVA*** d'Orbigny, 1854

TYPE SPECIES. *Reptomulticava pyriformis* d'Orbigny, 1854, designated herein; Valanginian, Ste Croix, Switzerland.

REMARKS. *Reptomulticava* was founded by d'Orbigny (1854) who assigned 12 described species (4 of them new) and a further 16 listed species to the genus. The type species of this genus is usually given as *Alveolites heteropora* Roemer, 1839 (e.g. Bassler 1953; Hillmer 1971), which appears to have been selected as the type by Gregory (1909*a*). However, as *Alveolites heteropora* is not among the 28 species assigned by d'Orbigny (1854) to *Reptomulticava* in his original description of this genus, it has no validity as the type species. Therefore, *Reptomulticava pyriformis* d'Orbigny, 1854 is here designated as the type species of *Reptomulticava*. *R. pyriformis*, redescribed by Walter (1972), was not only included in the original description of *Reptomulticava*, but it also seems to correspond with the general useage of the name *Reptomulticava* (e.g. Hillmer 1971; Hillmer, Gautier & McKinney 1975; Nye & Lemone 1978).

RANGE. Valanginian to ?Maastrichtian.

Reptomulticava brydonei (Gregory, 1909*b*)

Figs 140–143

?1854	*Reptomulticava collis* d'Orbigny: 1036; pl. 792, figs 1–3.
1909*b*	*Zonatula brydonei* Gregory: 64.
1909*a*	*Zonatula brydonei* Gregory; Gregory: 215; pl. 4, fig. 10.
1909*a*	*Ceriopora collis* (d'Orbigny); Gregory: 163; pl. 5, figs 5a–b.
1926	*Reptomulticava fungiformis* Gregory; Canu & Bassler: 29; pl. 24, figs 14–17 (?11–13).

HOLOTYPE. BM(NH) 10297, Mantell Colln, the single specimen described and figured by Gregory (1909*a, b*) as *Zonatula brydonei*.

OTHER MATERIAL. BM(NH) D52113–8, D52181 (sample), D52204–6, D52207 (sample), D52212 (sample), D55546–7, D57744, D57745 (thin section), D57746 (sample), D57747, D57753, Little Coxwell Pit, Pitt Colln; D52208 (sample), D57748–50, Faringdon Pit, Pitt Colln; D52209 (sample), Wicklesham Pit, Pitt Colln; D55325–7, Little Coxwell Pit, Gaster Colln; D55328 (sample), Little Coxwell Pit, Cleevely Colln; D55331, D57752 (sample), Little Coxwell Pit, Thomas Colln; D57751, Bowler's Pit, Pitt Colln.

DESCRIPTION. Zoarium (Fig. 140) of short, thick stems which are occasionally bifurcate, more rarely clavate, composed of tightly packed layers of stacked, basally growing subcolonies. Young zoaria (Fig. 141) are bun-shaped and unilamellar (described as *Ceriopora collis* by Gregory, 1909*a*).

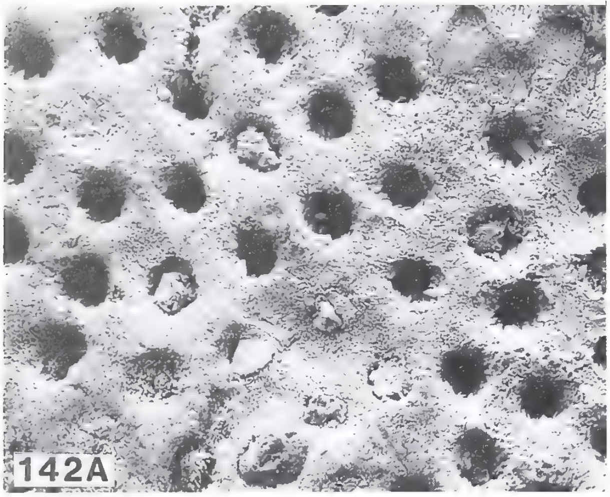
Autozooecia have circular apertures (Fig. 142), arranged in near quincunx, and are very thick-walled (wall thickness is commonly about the same as apertural diameter). Well-preserved autozooecia possess short, blunt mural spines within the apertures.

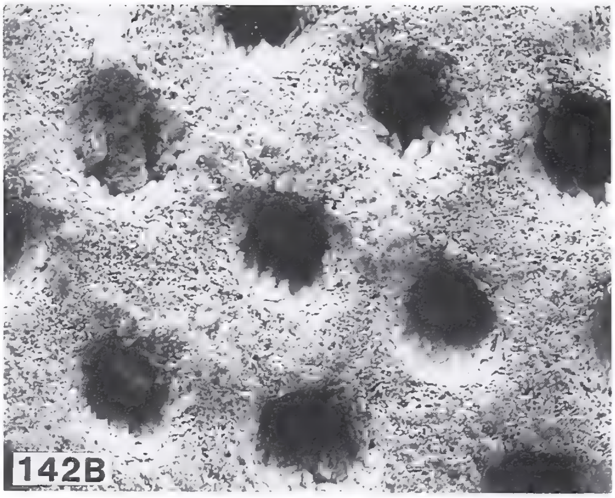
Kenozooecia are lacking.

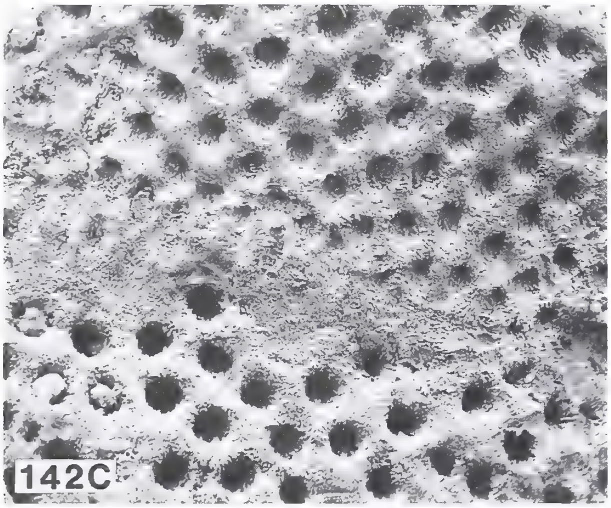
Brood chambers (Fig. 143) are uncommon, approximately circular in outline and about 1 mm in diameter, pierced by autozooecia which apparently support the roof of the chamber together with radial septa. The ooeciopore has not been observed.

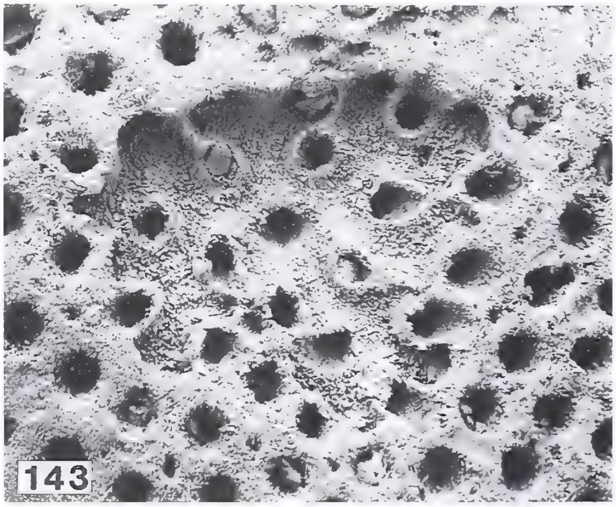
In thin section, the multilamellar form of the zoaria is clearly evident; each layer is about 0·9–1·3 mm in height, tapering towards the edges of the colony, and is generally formed by the coalescence of several subcolonies of independent origin. The 'pseudoancestrulae' at the focus of subcolonies continue upwards into the new daughter subcolony. Zooecial walls are thin proximally (close to the base of the subcolonies) but rapidly thicken distally where they may attain a thickness of 0·09 mm. Walls are indistinctly laminated and have a cloudy microstructure. Diaphragms are apparently absent or rare.

MEASUREMENTS. TAM, 0·08–0·10 mm.









Figs 142–143 *Reptomulticava brydonei* (Gregory). Fig. 142, BM(NH) 10297, holotype; 142A, × 65; 142B, thick-walled zooecia, × 152; 142C, edge of overgrowing subcolony, × 42. Fig. 143, BM(NH) D57744, worn gynozooecium, × 53.

REMARKS. *R. brydonei* is often mis-identified (e.g. Canu & Bassler 1926) as *Reptomulticava fungiformis* Gregory, 1909*b*, a species which is here regarded as a 'sclerosponge'. Although assigned to *Zonatula* Hamm, 1881 by Gregory (1909*b*), a more appropriate genus to accommodate this common Faringdon bryozoan is *Reptomulticava* d'Orbigny, 1854, a genus whose identity is discussed above. The type species of *Zonatula, Plethopora pseudotorquata* Hagenow, 1851 from the Maastrichtian, does not have zoaria constructed of a series of multilamellar subcolonies. Many species of *Reptomulticava* develop larger colonies than *R. brydonei* with a growth-form resembling that of *Semimulticavea marginata*.

Small colonies of *R. brydonei* may be found encrusting bivalve shells or sponges, but larger colonies are generally recovered detached from their substrata as short stems which are commonly worn. Zoarial morphology resembles that of *Tholopora* spp. from which *R. brydonei* can be distinguished by the absence of kenozooecia and the presence of extremely thick-walled autozooecia.

Genus ***THOLOPORA*** Gregory, 1909*a*

TYPE SPECIES. *Ceriopora clavata* Goldfuss, 1827, by original designation; Cenomanian, Essen, W. Germany.

REMARKS. Gregory (1909*a*) founded this genus to embrace compound 'Radioporidae' composed of superimposed subcolonies forming short, thick, blunt cylindrical stems. In it he placed seven species: *Ceriopora clavata* Goldfuss, 1827, the type species; *Ceriopora muletiana* d'Orbigny, 1850; *Domopora colligata* Gregory, 1909*b*; *Domopora polytaxis* (Hagenow, 1851)?, *sensu* Vine, 1885 (= *Domopora vinei* Gregory, 1909*b*); *Ceriopora stellata* (pars) Goldfuss, 1829 (= *Tholopora virgulosa* Gregory, 1909*b*); *Heteropora variabilis* (d'Orbigny 1852), *sensu* Novak, 1877 (= *Domopora novaki* Gregory, 1909*b*); and *Multicrescis variabilis* (d'Orbigny, 1854), *sensu* Gamble, 1896 (= *Domopora cantiana* Gregory, 1909*b*).

T. colligata (Gregory 1909*b*) was founded on one specimen (BM(NH) D7288), stated to be from Faringdon; but in the register it is listed as '?Faringdon, ?Baker Collection'. Unlike typical Faringdon Sponge Gravel, the matrix is greeny-grey and hard, and this suggests that the locality information is in error. There are no other Baker Colln Faringdon specimens in the BM(NH) but we know that Baker collected material from the Upper Greensand of Warminster which is of a similar lithology to Gregory's type specimen of *T. colligata*. There is no evidence that *T. colligata* actually occurs at Faringdon.

Canu & Bassler (1926) and Pitt (1949) misidentified Faringdon material as *T. virgulosa* (Gregory 1909*b*), another species originally described from the Upper Greensand of Warminster. *T. virgulosa*, redescribed by Voigt (1975), is here regarded as synonymous with *T. colligata*.

The present study has revealed the existence of three species of *Tholopora* at Faringdon: *T. dightoni* sp. nov., *T. hastingsae* sp. nov. and *T. thomasi* Pitt, 1949. The appearance of all three species in thin section is very similar, but external morphology reveals clear differences in the size and arrangement of the zooecial apertures.

RANGE. ?Hauterivian to ?Santonian.

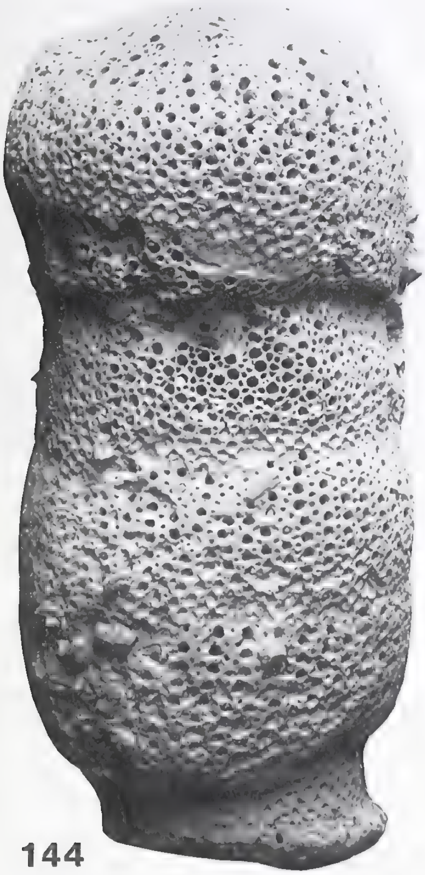


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Fig. 144 *Tholopora dightoni* sp. nov., BM(NH) D57672, **holotype**, × 15; see also Fig. 145.

Tholopora dightoni sp. nov. Figs 144–145

1926 · *Tholopora virgulosa* Gregory [*sic*]; Canu & Bassler: 63; pl. 20, fig. 1 [non *Tholopora virgulosa* (Gregory)].

HOLOTYPE. BM(NH) D57672, Little Coxwell Pit, Pitt Colln.

PARATYPES. BM(NH) D52161, D57664 (remnant & thin section), D57665 (remnant & thin section), D57666 (sample), D57667 (5), Little Coxwell Pit, Pitt Colln; D57673, Bowler's Pit, Pitt Colln; D57656 (sample), D57657 (3), D57660–1, Little Coxwell Pit, Thomas Colln; D57662, Faringdon Pit, Thomas Colln; D57663 (8), Little Coxwell Pit, Elliott Colln; D57664, Cleevely Colln.

NAME. For the late Dr H. Dighton Thomas, who originally suspected this to be a new species.

DESCRIPTION. Zoarium (Fig. 144) of short thick stems, up to 12 mm high, irregular in diameter (up to 6 mm) and composed of stacked, bun-shaped subcolonies, averaging 0·9 mm in height. Branching occurs but is rare.

Autozooecia are arranged regularly in uniserial connate rows, separated by kenozooecia, which radiate from subcolony centres (Fig. 145B). Autozooecial apertures are of moderate size, consecutive apertures within each row increasing in size centrifugally (i.e. towards the periphery of the subcolony). At high magnifications short mural spines (*c.* 0·006 mm long) can be seen inside the autozooecial apertures (Fig. 145C).

Kenozooecial apertures are small and have mural spines like those of the autozooecia but present in a slightly higher density.

The only brood chambers (Fig. 145D) observed are very small, broken, and roughly elliptical in outline. Occluded kenozooecia form the floor of the brood chamber, and some autozooecia pass through the chamber, presumably supporting the roof.

In thin section the wall microstructure is not distinctly laminated but is granular with dark patches which may be arranged in transverse bands resembling monilae. Interzooecial walls thicken gradually from the basal lamina of the subcolony upwards, attaining a maximum thickness of about 0·03 mm. A few probable basal diaphragms occur. The mode of origin of new subcolonies is not evident from the sections available, but the chambers of some centrally-located zooecia are seen to be continous from one subcolony to the next.

MEASUREMENTS (TAM and KAM measured from zooecia midway out from subcolony centres). TAM, 0·08–0·10 mm; KAM, 0·02–0·03 mm; GDL, 0·66 mm; GW, 1·2 mm.

REMARKS. This species is very similar to *T. thomasi* but differs in the significantly smaller dimensions of the zooecia and branch diameter. It is distinguished from *T. hastingsae* by the regular arrangement of autozooecia in rows and the larger size of the zooecia.

Tholopora hastingsae sp. nov. Figs 146–148

HOLOTYPE. BM(NH) D55336, Little Coxwell Pit, Pitt Colln.

PARATYPES. BM(NH) D52227, Faringdon Pit, Pitt Colln; D55120, D55335 (4), D57677–82, D55337–8 (4 thin sections), D57683 (thin section & remnant), D57684 (thin section & remnant), Little Coxwell Pit, Pitt Colln; D55344 (2 thin sections), D55346, Little Coxwell Pit, Thomas Colln; D55345 (2 thin sections), D57675–6, Little Coxwell Pit, Gaster Colln.

NAME. For the late Dr A. B. Hastings, bryozoologist wife of Dr H. D. Thomas for whom *T. thomasi* Pitt and *T. dightoni* sp. nov. are named.

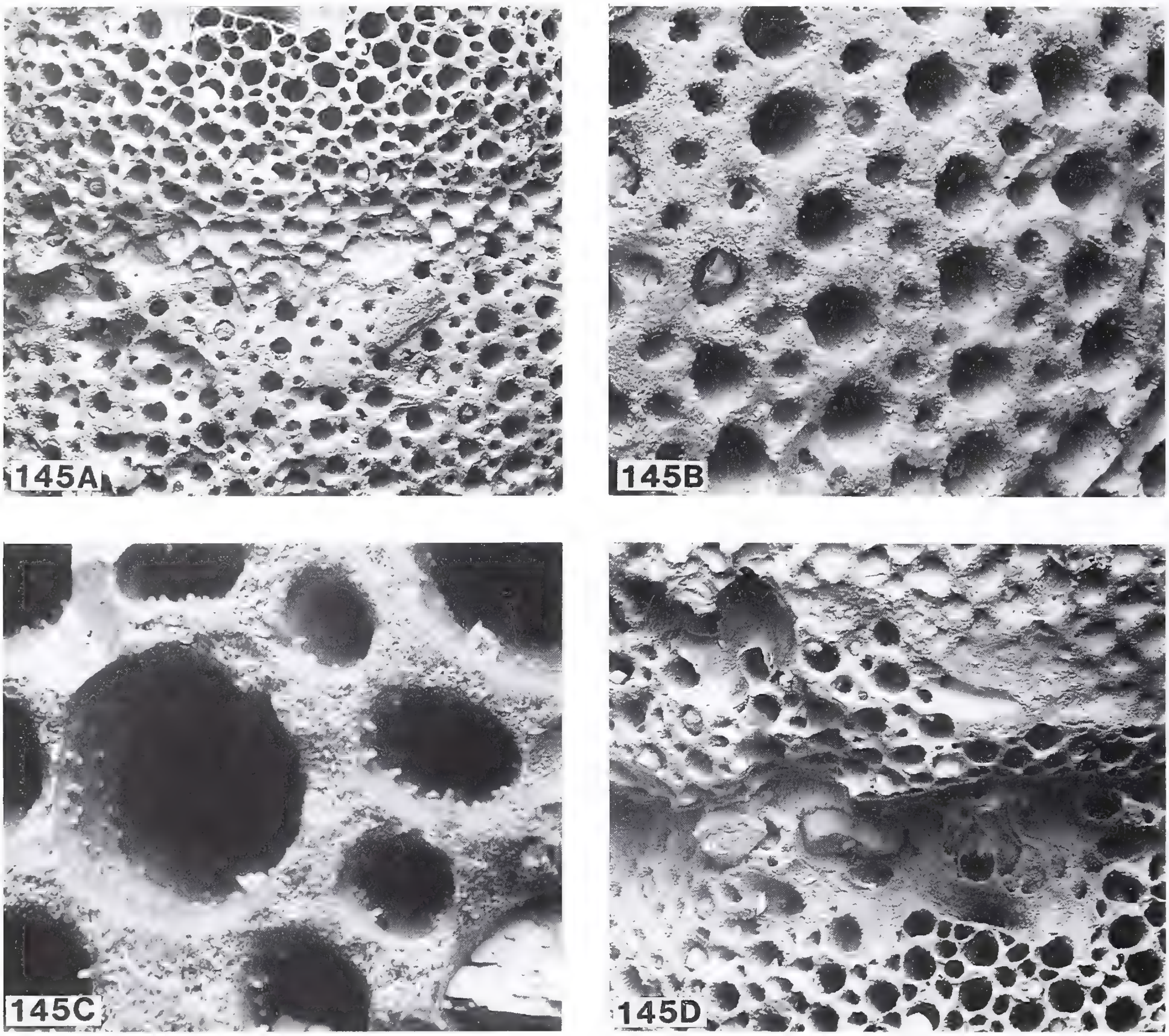


Fig. 145 *Tholopora dightoni* sp. nov., BM(NH) D57672, **holotype**; 145A, colony surface showing parts of two subcolonies, × 30; 145B, rows of autozooecia separated by kenozooecia, × 85; 145C, mural spines in autozooecia and kenozooecia, × 300; 145D, partly overgrown and broken gynozooecium, × 38; see also Fig. 144.

DESCRIPTION. Zoaria are short (Figs 146, 147A), generally less than 1 cm in height, and consist of a series of stacked bun-shaped subcolonies, sometimes bifurcating. Branches are typically 3–4 mm in diameter with annular constrictions between the subcolonies, each of which is about 0·9 mm in height. New subcolonies originate close to the centres of existing subcolonies and zooecial chambers may be continuous between parent and daughter subcolonies when seen in thin section.

Autozooecia are variable in size and arranged in irregular ill-defined radiating uniserial rows (Fig. 147B) separated by smaller kenozooecia, also irregularly arranged and variable in size. Within each row successive autozooecia are not always contiguous but may be separated by kenozooecia (cf. *T. thomasi* and *T. dightoni*). No mural spines have been observed, but details of fine preservation are obscured by secondary crystals of calcite in available material.

The single brood chamber observed (Fig. 148B) is roughly circular in outline, about 1·6–2·0 mm in diameter, with autozooecia passing through the chamber to support the roof together with internal vertical septa. The ooeciostome is not recognizable.

In thin section zooecial walls have a cloudy, granular appearance without obvious laminations. Dark transverse bands may occur which resemble monilae but the walls are parallel-sided. Exozonal wall thickness attains 0·03 mm. Of common occurrence are thin, aborally-flexed diaphragms (probable subterminal diaphragms) located 0·2–0·3 mm proximal of the zooecial aperture. Distinction between autozooecia and kenozooecia is not obvious in thin section.

MEASUREMENTS (measured from zooecia midway out from subcolony centres). TAM, 0·06–0·08 mm; KAM, 0·02–0·03 mm.

REMARKS. *T. hastingsae* is distinguished from *T. thomasi* and *T. dightoni* by the smaller size of the zooecial apertures and the less regular arrangement of the autozooecia which do not form such distinct rows and are not connate.

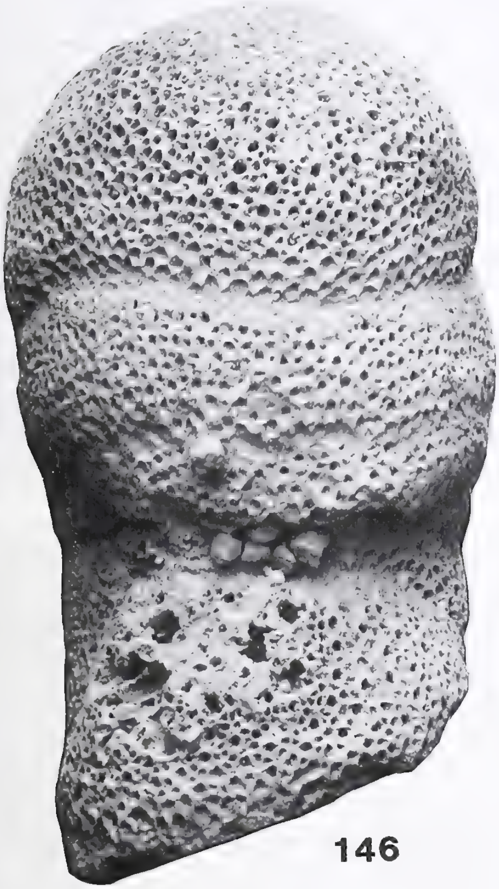


Fig. 146 *Tholopora hastingsae* sp. nov., BM(NH) D55336, **holotype**, × 22; see also Fig. 148.

Tholopora thomasi Pitt, 1949 Fig. 149

1949 *Tholopora thomasi* Pitt: 154; pl. 5, figs 1a, b; pl. 6.

HOLOTYPE. BM(NH) D37291, Little Coxwell Pit, Pitt Colln.

PARATYPES. BM(NH) D37292–3, Little Coxwell Pit, Pitt Colln. A third paratype is in the Treacher Colln, University of Reading.

OTHER MATERIAL. BM(NH) D47402, D55339, D55340, Little Coxwell Pit, Cleevely Colln; D52160 (sample), D55121, D57699 (sample), D57700 (thin section & remnant), D57701 (thin section), Little Coxwell Pit, Pitt Colln; D55341, D57697–8, Bowler's Pit, Thomas Colln; D55559, D57693–6, Little Coxwell Pit, Thomas Colln; D55342, Little Coxwell Pit, Wise Colln; D55343, D57685–90, Little Coxwell Pit, Gaster Colln.

DESCRIPTION. Zoaria are typically short (up to 12 mm), with thick branches which divide occasionally. The holotype colony is unusual in having a greatly expanded distal part formed by numerous closely-spaced branch divisions (Fig. 149A). Branches consist of a stack of bun-shaped subcolonies, each about 1·5 mm in height. The axial zone of the subcolonies comprises undifferentiated zooecia and is surrounded by a zone with well-defined, radiating uniserial rows of autozooecia separated by generally uniserial rows of kenozooecia. There can be as many as 50 radial rows of autozooecia in each subcolony.

Autozooecia have large rounded-polygonal apertures, those within a row being connate (Fig. 149B). Short mural spines can be seen within the apertures of well-preserved specimens (Fig. 149C).

Kenozooecial apertures are less than half the diameter of autozooecial apertures and are less rounded and more irregular in size. Short mural spines may be visible within kenozooecial apertures in slightly higher densities than in the autozooecia.

Brood chambers (Fig. 149D) have only been observed broken, lacking roof and ooeciopore. They are digitate in outline shape, with lobes parallel to the rows of kenozooecia, indented marginally by autozooecia.

In thin section the zooecial walls have a cloudy, granular appearance without distinct laminations. Transverse bands of darker material resemble monilae, but zooecial walls are apparently parallel-sided. Wall thickness increases markedly in the exozones of subcolonies where it may attain 0·06 mm. Basal, older subcolonies have thicker walls than younger subcolonies. Thin, aborally-flexed diaphragms are sporadically developed. Many zooecial chambers in the axial parts of subcolonies are continuous between succesive subcolonies, and budding by intrazooecial fission apparently contributed to the formation of new subcolonies.

MEASUREMENTS (measured from zooecia midway out from subcolony centres). TAM, 0·16–0·20 mm; KAM, 0·05–0·08 mm.

REMARKS. This is the commonest of the three species of *Tholopora* at Faringdon and is distinguished from the other two by the larger size of the autozooecia.

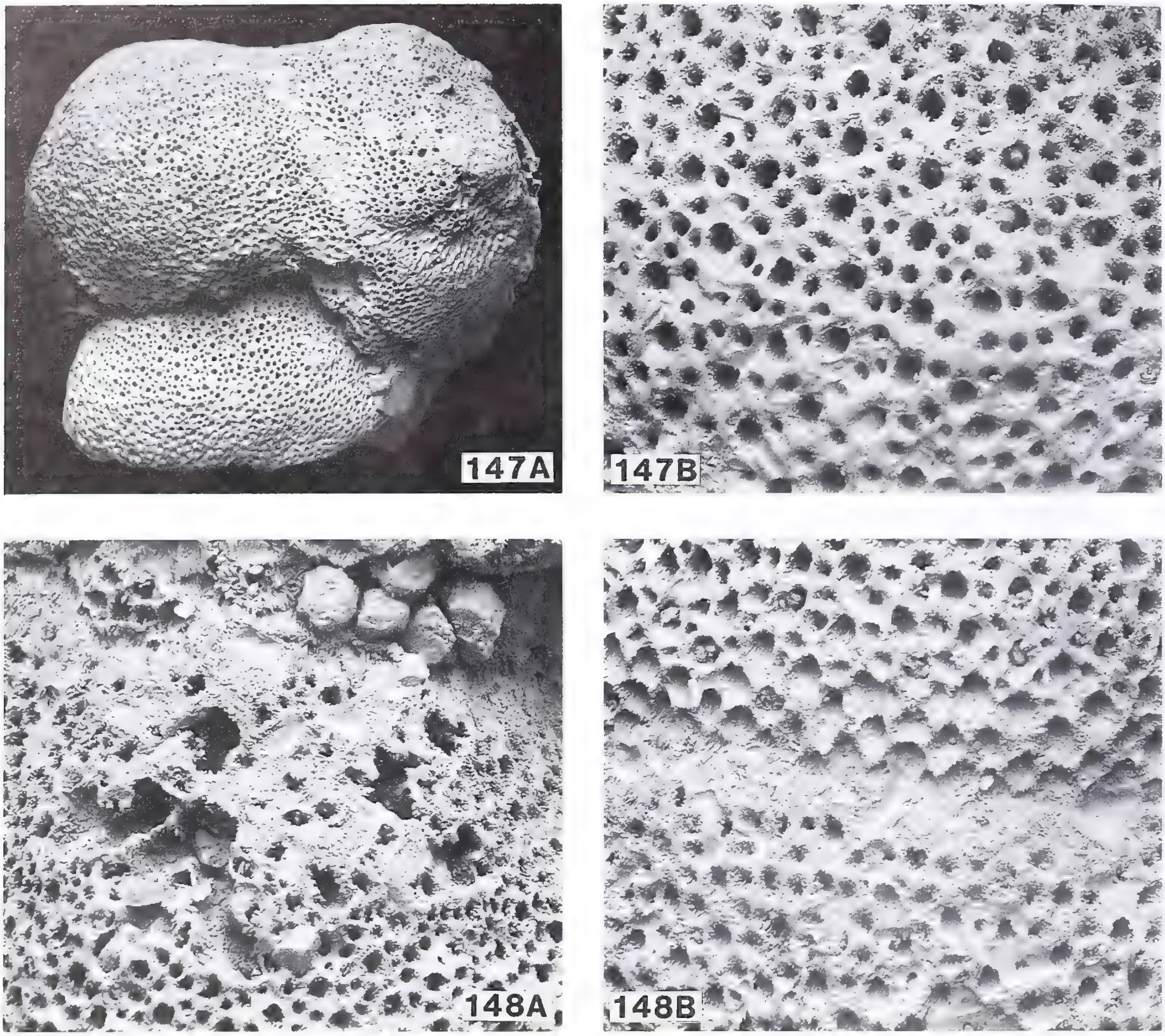
Suborder **CANCELLATA** Gregory, 1896
Family **HORNERIDAE** Gregory, 1899

Genus ***SIPHODICTYUM*** Lonsdale, 1849

TYPE SPECIES. *Siphodictyum gracile* Lonsdale, 1849, by monotypy; Atherfield Clay (Aptian), Isle of Wight.

REMARKS. The distinction between *Siphodictyum* and the well-known Tertiary to Recent genus *Hornera* Lamouroux, 1821 (see Mongereau, 1972), is not firmly established. The two genera share a vinculariiform colony morphotype with autozooecia opening on one side only of the branches, cancelli between the autozooecial apertures, and gynozooecia on branch reverse sides with roofs of calcified interior wall. Canu & Bassler (1926) removed *Siphodicytum* from the Family Horneridae, to which it had been assigned by Gregory (1899), and transferred it to the Family Ascosoeciidae because they wrongly thought that the gynozooecium was perforated by zooecial tubes. However, some other differences do exist between *Hornera* and *Siphodictyum*: in the type species of *Hornera*, *Hornera frondiculata* Lamouroux, the zooecia are arranged in distinct longitudinal rows; the presence of the subapertural pore described below for *Siphodictyum* has yet to be demonstrated in *Hornera*; and whereas *Siphodictyum* has a bushy colony-form, the branches of *Hornera* are generally arranged in planar fans.

As the type species of *Semicellaria* d'Orbigny, 1853 (= *Hemicellaria* d'Orbigny, 1850), *S. ramosa* d'Orbigny, is a subjective junior synonym of the type species of *Siphodictyum*, d'Orbigny's genus is placed in synonymy with Lonsdale's.



Figs 147–148 *Tholopora hastingsae* sp. nov. Fig. 147, BM(NH) D55120; 147A, bifurcating stem, × 10; 147B, autozooecia arranged crudely in rows, × 50. Fig. 148, BM(NH) D55336, **holotype**; 148A, poorly-preserved gynozooecium; 148B, edge of overgrowing subcolony, × 54; see also Fig. 146.

RANGE. Lower Cretaceous (Barremian to Aptian).

Siphodictyum gracile Lonsdale, 1849 Figs 150–153

1847 *Cricopora gracile* Fitton: 302 (name only).
1849 *Siphodictyum gracile* Lonsdale: 94; pl. 5, figs 16–23.
1850 *Hemicellaria ramosa* d'Orbigny: 86.
1853 *Semicellaria ramosa* (d'Orbigny) d'Orbigny: 935; pl. 772, figs 11–14.
1899 *Siphodictyum gracile* Lonsdale; Gregory: 363; pl. 12, figs 14–15.
1926 *Siphodictyum gracile* Lonsdale; Canu & Bassler: 87; pl. 14, figs 14–21.
1926 *Siphodictyum irregulare* Canu & Bassler: 89; pl. 14, figs 1–11.
1971 *Siphodictyum gracile* Lonsdale; Walter & Busnardo: 96; pl. 7, figs 1–10.
1974 *Siphodictyum gracile* Lonsdale; Masse & Walter: 191; pl. 36, figs 2–3.
1975 *Siphodictyum gracile* Lonsdale; Walter *et al.*: 111; pl. 9, figs 10–11.
1975 *Siphodictyum irregulare* Canu & Bassler; McKinney: 72; pl. 3, fig. 1.
1977 *Siphodictyum gracile* Lonsdale; Walter: 328; pl. 1, fig. 2.
1979 *Siphodictyum gracile* Lonsdale; Walter & Clavel: 822; pl. 2, figs 5–7.
1981 *Siphodictyum gracile* Lonsdale; Voigt: 441; figs 1A–B.
1984 *Siphodictyum gracile* Lonsdale; Delamette & Walter: 34; pl. 11, figs 7, 9.

HOLOTYPE. BM(NH) 46804, Atherfield Clay (Aptian), Atherfield, Isle of Wight, Morris Colln.

OTHER MATERIAL. BM(NH) D55107, D55108, D55334, D57946–7, Little Coxwell Pit, Gaster Colln; D55109, D55332 (sample), D55255 (5), Little Coxwell Pit, Thomas Colln; D37322–3, D52215 (sample), D55333 (sample), D57635,

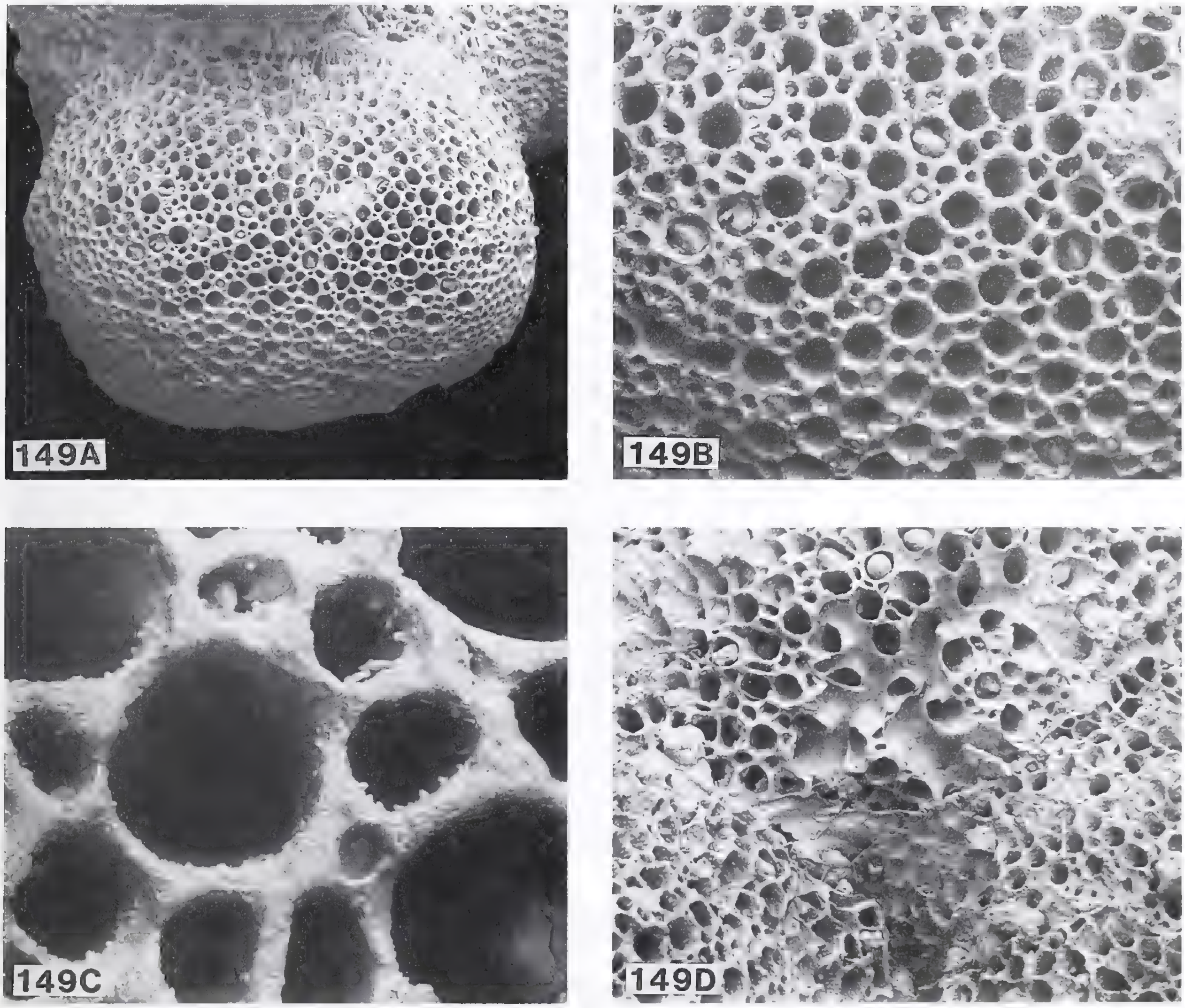


Fig. 149 *Tholopora thomasi* Pitt, BM(NH) D37291, holotype; 149A, × 16; 149B, autozooecia and kenozooecia, × 30; 149C, short mural spines visible within zooecial apertures, × 160; 149D, worn gynozooecium, × 22.

Little Coxwell Pit, Pitt Colln; D57639–41, Little Coxwell Pit, Elliott Colln; D57642, Davis Colln. USNM 69944 (including 3 thin sections also registered as 248243), syntypes of *S. irregulare* Canu & Bassler, 1926.

Description. Zoarium arborescent, of narrow (mean diameter *c.* 0·6 mm) cylindrical branches (vinculariiform), which bifurcate dichotomously; successive bifurcations usually occur in slightly different planes with the result that the colony is a 3-dimensional bush rather than a planar fan. Branch anastomoses are rare. The colony base is a slightly expanded cone.

Autozooecial apertures open on one side only of the branch (the obverse) and are arranged sometimes in transverse rows, sometimes in approximate quincunx (Fig. 150A). They are small, circular to slightly longitudinally elongate, and may have a gently raised rim (Fig. 150B). In exceptionally well preserved specimens, blunt mural spines may be visible within the apertures, and a minute 'subapertural pore' (*c.* 0·01–0·02 mm) can be observed just proximally of the aperture (Fig. 150C).

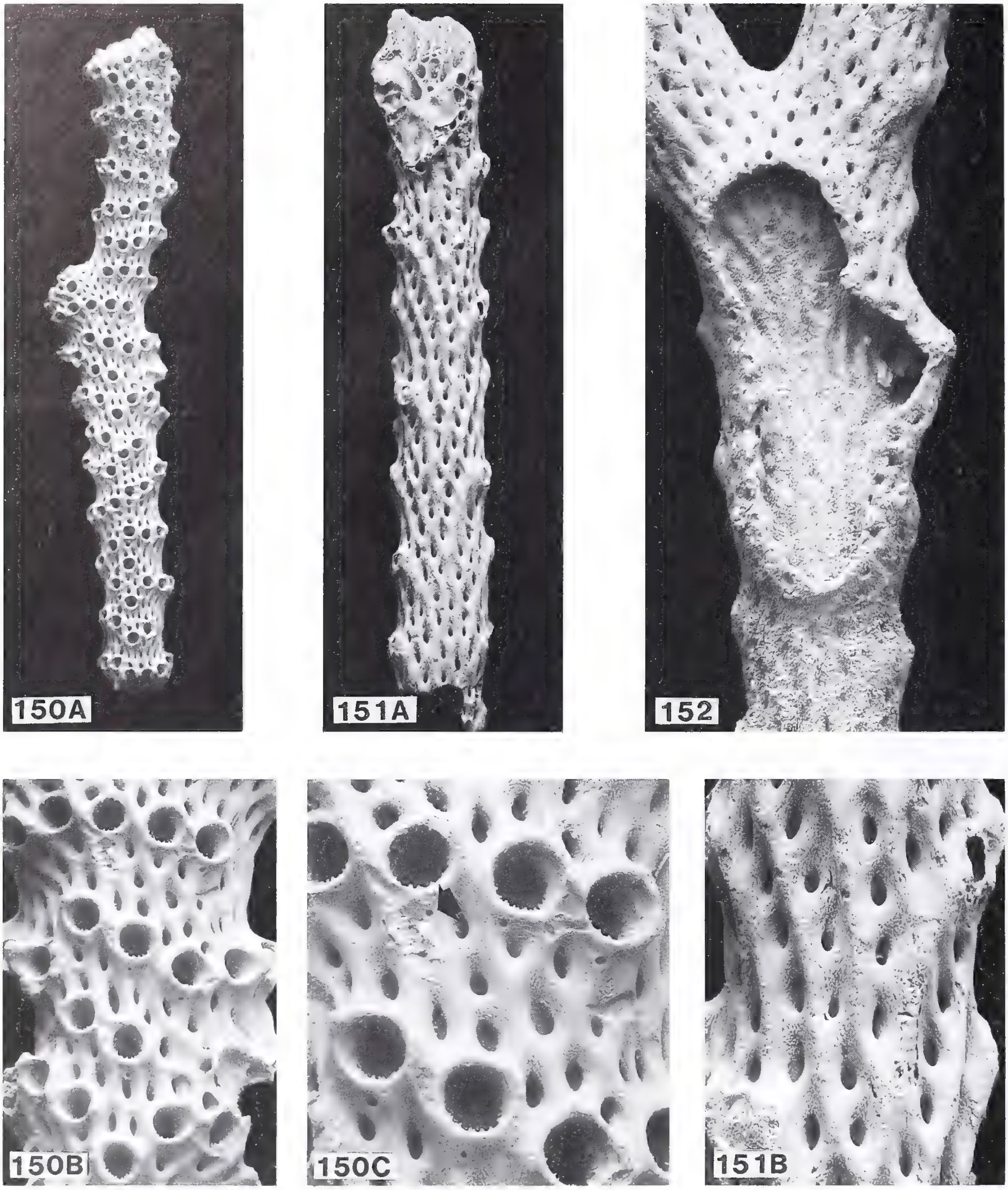
Cancelli occupy the reverse sides of branches (Fig. 151) and the areas between autozooecial apertures on the obverse sides of branches (Fig. 150C). They have small, thick-walled apertures, often rather longitudinally elongated and often funnel-shaped. The arrangement of cancelli on the branch obverse may be in longitudinal lines.

The gynozooecium (Fig. 152) is a longitudinally elliptical, bulbous swelling situated on the branch obverse which may bifurcate if positioned over a branch division. The roof of the gynozooecium is formed of porous apparent interior wall calcification resembling cancelli, and a calcified lamina forms the floor. The ooeciopore is distal, large and transversely elliptical.

In thin section (Fig. 153) branches are seen to have thin-walled endozones surrounded by exozones with thick, laminated walls.

Measurements. TAM, mean 0·06 mm; GDL, up to 0·40 mm; GW, up to 0·25 mm; LOSM, 0·04 mm; TOSM, 0·14 mm.

Remarks. Fitton's (1847) specific name for this species was later adopted by Lonsdale (1849) when validly describing the



Figs 150–152 *Siphodictyum gracile* Lonsdale. Fig. 150, BM(NH) D55107; 150A, obverse side of branch, × 23; 150B, × 64; 150C, detail showing subapertural pores (one is arrowed), × 130. Fig. 151, BM(NH) D57946; 151A, reverse side of branch, × 33; 151B, detail showing cancelli, × 90. Fig. 152, BM(NH) D57947, gynozooecium located on branch reverse and lacking a frontal wall, × 47.

species for the first time as *Siphodictyum gracile*. As Fitton merely mentioned the species without description, definition or indication, his citation does not constitute a valid publication of *gracile* because it fails to satisfy Article 12 of the Code of Zoological Nomenclature.

Lonsdale's type specimen (BMNH 46804) from the Atherfield Clay of the Isle of Wight is a large arborescent colony of closely-packed branches embedded in matrix. Branch diameter is a little greater than in most Faringdon specimens but zooecial characteristics appear identical. *S. irregulare* Canu & Bassler does not differ significantly from *S. gracile*; slight variations in the arrangement of apertures of the type

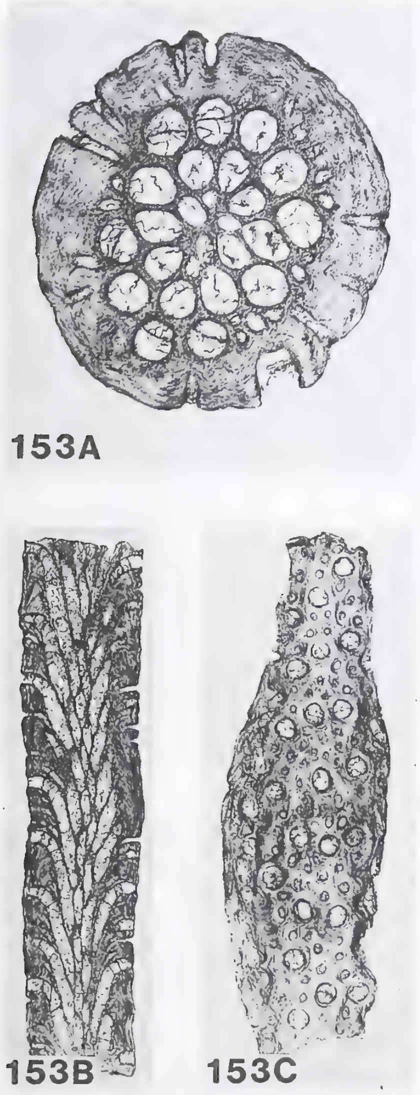


Fig. 153 *Siphodictyum gracile* Lonsdale, USNM 248243, syntype thin sections of *S. irregulare* Canu & Bassler; 153A, transverse section, × 70; 153B, longitudinal section, × 21; 153C, shallow tangential section, × 34.

used to distinguish *S. irregulare* are unsuitable for species discrimination in *Siphodictyum*.

The slender branches of this species are common at Faringdon, and the species is widely distributed in the Barremian and Aptian of Europe. It is distinguished from the similar *Laterocavea? intermedia* Canu & Bassler by the confinement of the autozooecial apertures to one side of the branches whereas they occur on two sides in *L.? intermedia*.

Family **PETALOPORIDAE** Gregory, 1899

Genus ***LATEROCAVEA*** d'Orbigny, 1853

TYPE SPECIES. *Laterocavea dutempleana* d'Orbigny, 1853, by subsequent designation of Canu & Bassler, 1926; Albian of Grandpré.

REMARKS. *Laterocavea* is a cancellate genus characterized by a slight flattening of the branches with autozooecia opening on both sides (cf. *Siphodictyum*, p. 133). Gregory (1899) regarded *Laterocavea* as a synonym of *Hemicellaria* d'Orbigny, 1850 (=*Semicellaria* d'Orbigny, 1853). However, the type species of *Hemicellaria, H. ramosa* d'Orbigny, has an 'eccentric bifoliate' colony-form (*sensu* McKinney 1986) with branches which possess a distinct upper surface, as in genera such as *Reticulipora* and the cystoporates *Goniocladia* and *Ramipora* (see Utgaard *in* Boardman *et al.* 1983).

RANGE. Aptian to Albian, ?Campanian; it is unclear whether a second, U. Cretaceous species, *L. punctata* (d'Orbigny) which was attributed by d'Orbigny (1850) to his genus, is really congeneric with *L. dutempleana*.

Laterocavea dutempleana d'Orbigny, 1853

Figs 154–156

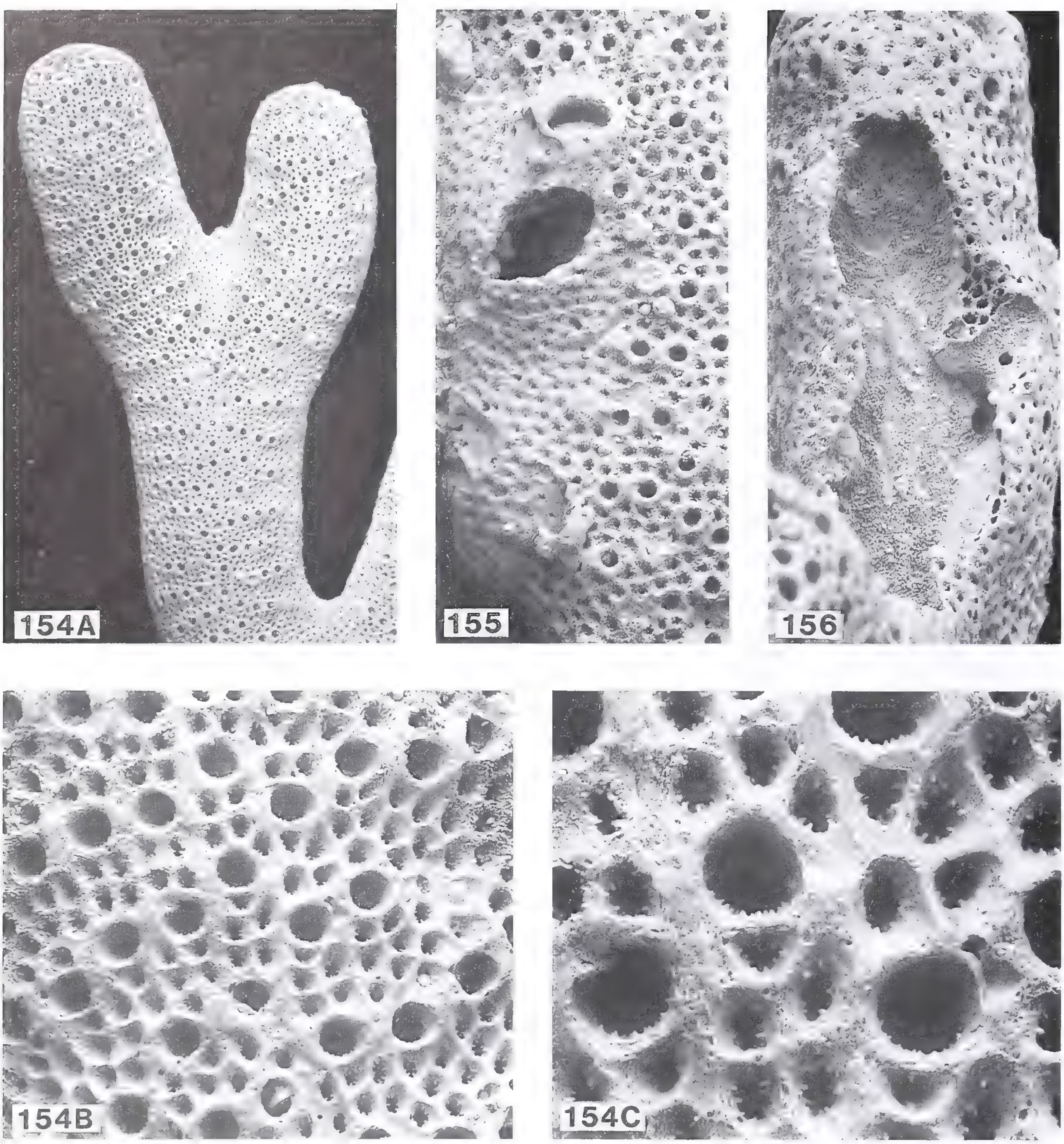
1853	*Laterocavea dutempleana* d'Orbigny: 933; pl. 772, figs 7–10.
1889	*Idmonea dutempleana* (d'Orbigny) Pergens: 350.
1899	*Hemicellaria dutemplei* (d'Orbigny); Gregory: 370.
1899	*Petalopora cunningtoni* Gregory: 376; pl. 12, figs 11–13.
1926	*Laterocavea dutempleana* d'Orbigny; Canu & Bassler: 85; pl. 15, figs 1–6.
1977	*Laterocavea dutempleana* d'Orbigny; Walter: 329; pl. 1, figs 3, 6.
1979	*Laterocavea dutempleana* d'Orbigny; Walter & Clavel: 821; pl. 2, figs 1, 3, 4, 10.
1981	*Laterocavea dutempleana* d'Orbigny; Voigt: 441; fig. 1c–d.

MATERIAL. BM(NH) D5130 (specimen and thin section), D7104, Cunnington Colln, figd syntypes of *Petalopora cunningtoni* Gregory (1899: pl. 12, figs 12 & 13 respectively); D55100, D55248, D55251 (3), D55252 (peel), D57644 (sample), D57709–10, D57948, Little Coxwell Pit, Pitt Colln; D55246 (sample), D55247 (sample), D57708 (6), Little Coxwell Pit, Thomas Colln; D55249 (sample), D55250, Little Coxwell Pit, Gaster Colln; D55253, Little Coxwell Pit, Cleevely Colln; D55254, collection and locality unknown.

DESCRIPTION. Zoarium erect, arborescent, with slightly compressed branches (Fig. 154A) which are ovate in transverse section, 1·5 to 1·8 mm wide. The colony base is a low cone of circular cross section. The surface of the base and proximal parts of the first branch are covered entirely with cancelli which are slit-like and aligned in vertical rows parallel to growth direction. Successive branch dichotomies are usually in the same plane as branch compression, and the two daughter branches of a dichotomy may bend towards one another until subparallel.

Autozooecia open on the two wide faces of the branches, their apertures arranged more-or-less in transverse rows (Fig. 154B), often with an offset along the midline of each face. Autozooecial apertures are small, circular or transversely elliptical, have a slightly raised rim and may be contiguous with laterally adjacent apertures in the same transverse row. Blunt mural spines are visible within the autozooecial apertures of well-preserved specimens (Fig. 154C).

Cancelli occupy the areas between autozooecial apertures, the entire surface of the narrow edges of the branches, and the basal parts of colonies. They are small (*c.* 0·03 mm in diameter), rounded polygonal in outline shape, sometimes longitudinally elongate and funnel-like, tapering inwards



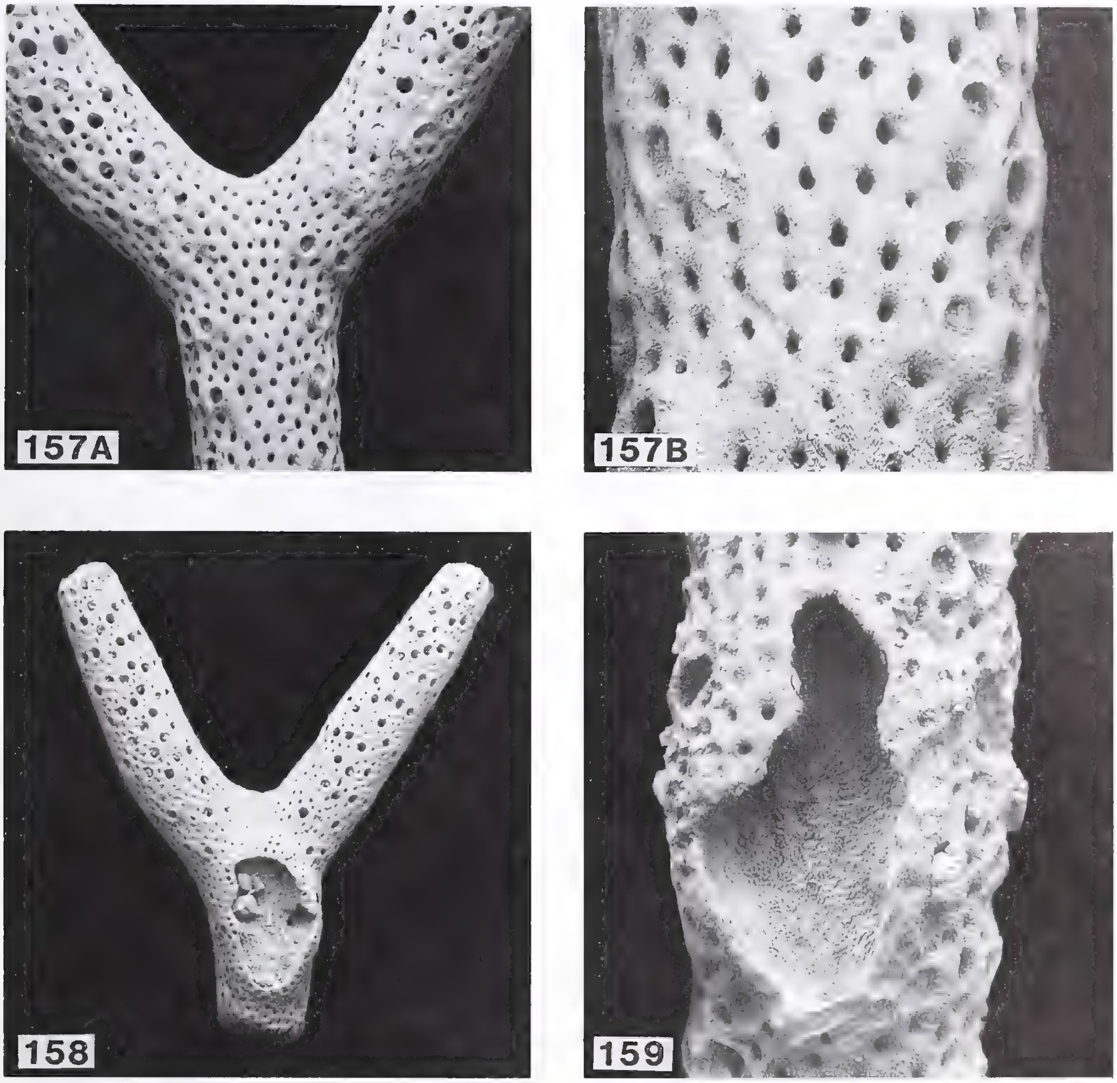
Figs 154–156 *Laterocavea dutempleana* d'Orbigny. Fig. 154, BM(NH) D57948; 154A, bifurcating branch with growth tips, × 15; 154B, autozooecia and cancelli, × 71; 154C, short mural spines visible within apertures of autozooecia and cancelli, × 210. Fig. 155, BM(NH) D55709, gynozooecium with well-preserved frontal wall and ooeciopore, × 39. Fig. 156, BM(NH) D55250, gynozooecium with abraded frontal wall, × 47.

from the colony surface. Blunt mural spines occur within the cancelli and are somewhat larger than those in the autozooecia (Fig. 154C).

Gynozooecia (Figs 155–156) are situated on the narrow faces of the branches or close to the edges of the broad faces. They are large and longitudinally elongate, form a slight swelling of the branch, and have a frontal wall composed apparently of cancelli which are smaller in size than normal cancelli. The floor of the gynozooecium (Fig. 156) appears to be formed of a calcified interior wall which is penetrated in one example (BM(NH) D55250) by a pore the size of an autozooecial aperture situated near the chamber edge about mid-length; this may represent the proximal part of the fertile zooecium. The ooeciopore is located distally and is large, transversely elongate and crescent-shaped owing to the occurrence of a curved internal platform which indents its proximal edge (Fig. 155).

MEASUREMENTS. TAM, 0·05–0·06 mm; TPM, 0·08–0·10 mm; GDL, up to 2·0 mm; GW, up to 1·0 mm; TOPM, 0·25 mm; TOSM, 0·40 mm.

REMARKS. *Laterocavea dutempleana* was first described from



Figs 157–159 *Laterocavea? intermedia* Canu & Bassler. Fig. 157, BM(NH) D55102; 157A, bifurcating branch, × 26; 157B, alveoli, × 77. Fig. 158, USNM 69942a, **lectotype** (herein selected), bifurcating branch with worn gynozooecium, × 14. Fig. 159, BM(NH) D57937, worn gynozooecium, × 63.

the Albian of Grandpré. D'Orbigny's type specimen could not be located at the MNHN during May 1985, although a tablet (numbered 6027) bearing the appropriate label but with no specimen attached was found.

Gregory (1899) did not record *Laterocavea dutempleana* from Faringdon but described a new species, *Petalopora cunningtoni*, which is undoubtedly a junior synonym of *L. dutempleana*. There are 3 syntypes of *P. cunningtoni*, two from Faringdon (BM(NH) D5130, D7104) and one (BM(NH) D2301) in an argillaceous matrix from an unknown locality. BM(NH) D7104 is herein chosen as the lectotype of *P. cunningtoni*.

Laterocavea? intermedia Canu & Bassler, 1926

Figs 157–159

1926 *Laterocavea intermedia* Canu & Bassler: 86; pl. 13, figs 9–17.
1926 *Clausa cranei* Canu & Bassler: 79; pl. 17, figs 6–7.

LECTOTYPE. USNM 69942a, selected herein, the specimen figured by Canu & Bassler 1926: pl. 13, figs 16–17.

PARALECTOTYPES. USNM 69942b–k, the remaining syntypes, some of which were figured by Canu & Bassler (1926).

MATERIAL. BM(NH) D55249 (2), D55101 (3), D55102, Little Coxwell Pit, Gaster Colln; D55255, D55485, Little Coxwell Pit, Thomas Colln; D55256 (5), D55257, D55636, Little Coxwell Pit, Pitt Colln; D57643 (2), D57937, Little Coxwell Pit, Davis Colln; D55638, Little Coxwell Pit, Elliott Colln.

DESCRIPTION. Zoarium erect, vinculariiform (Figs 157A, 158), with narrow cylindrical branches, 0·6–0·9 mm in diameter. Autozooecia open on two opposite faces of the branch with longitudinal cancelli occupying the strips between. Branches bifurcate in the plane formed by joining the two autozooecial faces (i.e. at right angles to the plane formed by joining the two cancellate faces). Successive bifurcations are often in a plane at right angles to one another, the distribution of autozooecia and cancelli reversing after the division. The colony base is a slightly expanded cone with the surface and lower part of the stem composed of cancelli.

Autozooecial apertures are small, circular or slightly longitudinally elongated, and often arranged in transverse rows, adjacent apertures being connate. Apertural rims are slightly raised, and terminal diaphragms may occur. Well-preserved autozooecia reveal the presence of a minute subapertural pore just proximal of the aperture.

Cancelli occupy the branch surface between transverse rows of autozooecial apertures, and form the edge strips (Fig. 157B) and colony base. They are small (about 0·03 mm in diameter) and circular or a little longitudinally elongated.

The gynozooecium (Figs 158–159) is a bulbous, longitudinally elongate swelling developed on a cancellate branch face, bifurcating if coincident with a branch division, and with the edges occasionally digitate. Broken roofs, apparently formed of cancelli, reveal a calcified floor which in some cases contains an opening, midlength and close to the edge of the chamber, possibly representing the proximal part of the fertile zooecium. The ooeciopore is situated distally, and is large and transversely elongate.

MEASUREMENTS. TAM, 0·07–0·09 mm; GDL, 1·20–1·60 mm; GW, 0·40–0·45 mm; LOSM, 0·06 mm; TOSM, 0·18 mm.

REMARKS. Walter & Clavel (1979) regarded *L. intermedia* as a junior synonym of *Siphodicytum gracile* Lonsdale (see p. 134). The two species undoubtedly have many features in common, notably the subapertural pore and the overall form of the gynozooecium, but there appear to be consistent differences in the distribution of the cancelli (on the branch obverse in *S. gracile*, and on the two opposite lateral branch faces in *L.? intermedia*) and branching pattern (successive branch bifurcations being in subparallel planes in *S. gracile* but commonly in perpendicular planes in *L.? intermedia*). No colonies have been found of intermediate type or having a mixture of the characters of the two species.

Whereas the distribution of the cancelli favours assignment of the species to *Laterocavea* in the Family Petaloporidae, the presence of the subapertural pore suggests a closer relationship with *Siphodictyum* which is placed in the Family Horneridae. Pending a better understanding of familial concepts in cancellates, a conservative policy is adopted here and the species is questionably retained within *Laterocavea*.

This is a rare species at Faringdon and is apparently unknown elsewhere. It is distinguished from *L. dutempleana* by the distribution of the autozooecia and cancelli, the circular section of the branches and the right-angle branching pattern.

Family **CYTIDIDAE** d'Orbigny, 1854

Genus ***ECHINOCAVA*** d'Orbigny, 1854

TYPE SPECIES. *Ceriopora raulinii* Michelin, 1841, by monotypy; Albian of Grandpré, Belgium.

REMARKS. *Echinocava* is distinguished by the dendroid colony branches on which are situated raised autozooecial fascicles, approximately subcircular in outline, separated by areas of apparent cancelli.

D'Orbigny (1850) first described this genus as *Echinopora*, assigning to it only Michelin's (1841) species *Ceriopora raulinii* (as *Echinopora raulini*; deletion of the second 'i' in *raulinii* is an unjustified amendment of Michelin's original specific name).

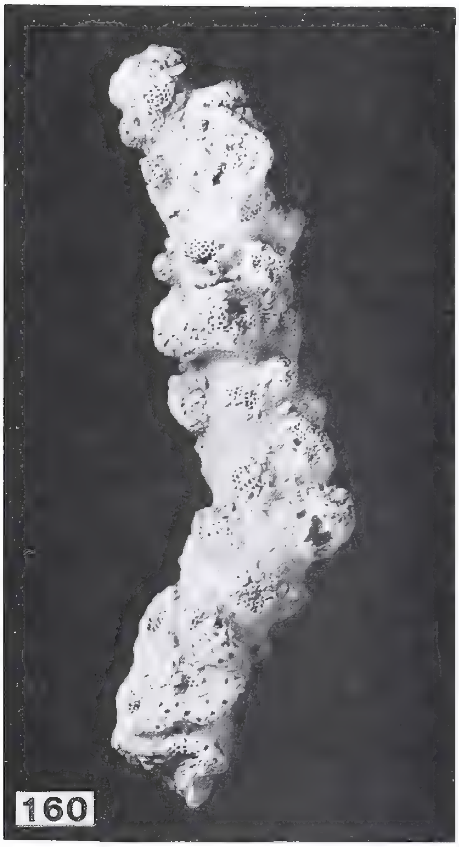


Fig. 160 *Echinocava raulinii* (Michelin), BM(NH) D55103, optical photograph of a colony branch, × 5·3.

Echinopora d'Orbigny, 1850 is a junior homonym of *Echinopora* Lamarck, 1816; this homonymy was later (1854) recognized by d'Orbigny himself who proposed the replacement name *Echinocava* and redescribed for a second time Michelin's species from the Albian of Grandpré.

Voigticytis Walter, 1986, type species *Cyrtopora campicheana* d'Orbigny, 1853 from the Valanginian of Ste Croix, Switzerland, is here regarded as a subjective junior synonym of *Echinocava*. The only important difference between the type species of the two genera appears to be the longitudinal ridges formed by the walls of the cancelli in *V. campicheana*.

The presence of cancelli together with brood chambers roofed by interior wall (Walter 1986: pl. 9, fig. 6) implies that *Echinocava* belongs to the Suborder Cancellata.

RANGE. Valanginian to Albian.

Echinocava raulinii (Michelin, 1841) Figs 160–163

1841 *Ceriopora raulinii* Michelin: 2; pl. 1, figs 7a, b.
1850 *Echinopora raulini* (Michelin) d'Orbigny: 141.
1854 *Echinocava raulini* (Michelin) d'Orbigny: 1013; pl. 788, figs 7–8.
1883 *Ceriopora (Echinocava) raulini* Michelin; Keeping: 139.
1926 *Plethopora aptensis* Canu & Bassler: 53; pl. 7, figs 3–4.
1974 *Echinocava raulini* (Michelin); Masse & Walter: 194; pl. 788, figs 7–8.
1981 *Plethopora aptensis* Canu & Bassler; Voigt: 441, fig. 1g.

1984 *Echinocava raulini* (Michelin); Delamette & Walter: 35; pl. 5, fig. 5.

1984 *Plethopora* cf. *aptensis* Canu & Bassler; Delamette & Walter: 35; pl. 5, fig. 7.

MATERIAL. BM(NH) D52195 (3), D55306, Little Coxwell Pit, Pitt Colln; D55103, D57727 (3 thin sections), D57949–50, Little Coxwell Pit, Thomas Colln; D55301, Little Coxwell Pit, Elliott Colln; D57652–5, Davis Colln. USNM 69903, 5 syntypes of *Plethopora aptensis* Canu & Bassler, 1926. OUM K.82, K.83, Davey Colln.

DESCRIPTION. Zoarium of thick dendroid branches (Figs 160–161), occasionally bifurcating, astogenetically variable in diameter (1·5–6 mm), with blunt rounded growth tips. The autozooecia are in fascicles (Fig. 163A), about 1 mm in diameter, subcircular in outline and projecting above the general level of the colony surface as rounded mamelons; the remainder of the colony surface is covered with cancelli (Fig. 162).

Autozooecial apertures are polygonal and increase in size towards the centre of the fascicle. Outer parts of autozooecia are directed distally up the branch.

Cancelli have small funnel-shaped, subcircular apertures and thick walls (Fig. 163B).

Thin sections show that the autozooecia are long, slender tubes budded within branch endozones, whereas cancelli are very short tubes budded close to the branch surface within the exozone. No diaphragms have been observed. The microstructure of the zooecial wall is amorphous and cloudy in appearance without distinct lamination, but the thick walls of the kenozooecia have laminations subparallel to the colony surface.

An apparent brood chamber is present on the proximolateral side of a fascicle in BM(NH) D57949 (Fig. 163C). It is a convex swelling roofed by cancellate interior wall. A hole within the structure may be a broken and enlarged ooeciopore.

MEASUREMENTS. TAM (at centre of fascicle), *c.* 0·12 mm; cancelli diameter, 0·02–0·06 mm.

REMARKS. This is a comparatively rare species at Faringdon which was described as *Plethopora aptensis* by Canu & Bassler (1926). However, to judge by the figures of Michelin (1841), *P. aptensis* is a junior synonym of Michelin's species *Ceriopora raulinii* from the Albian of Grandpré. Unfortunately, Michelin's types appear to be lost; they were not mentioned by Walter (1975) in his revision of Albian and Cenomanian bryozoans from the Michelin Collection in the MNHN. *E. raulini* is recorded also from the Barremian and Aptian of SE France (Masse & Walter 1974; Delamette & Walter 1984), and Aptian of Upware, Cambridgeshire (Keeping 1883).

Available material from Faringdon is often worn. In extreme cases of wear, the autozooecial fascicles may be hollowed out and left as depressions on the colony surface (cf. Delamette & Walter 1984: pl. 5, fig. 5). This pattern of wear, which results in colonies with a coral-like appearance, presumably reflects the thicker calcification of the surrounding cancelli.

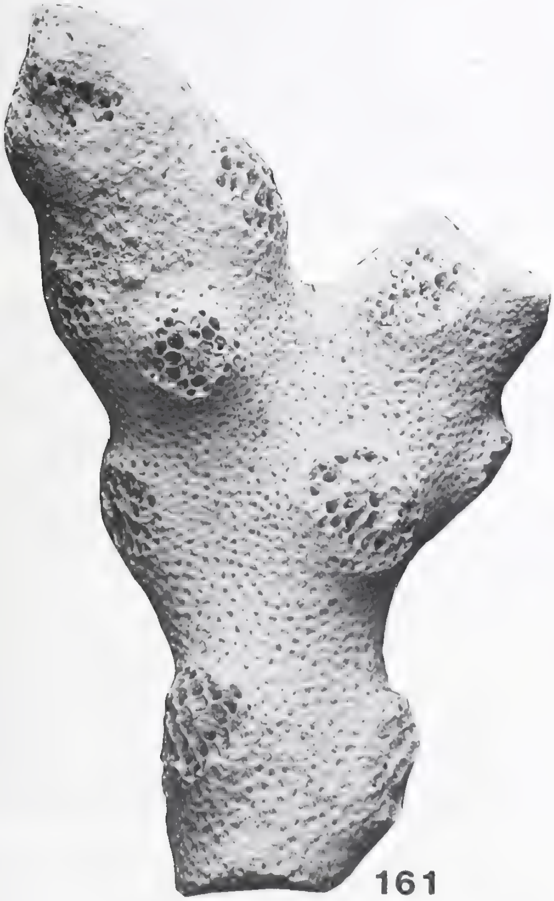


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Fig. 161 *Echinocava raulinii* (Michelin), USNM 69903a, syntype of *Plethopora aptensis* Canu & Bassler, × 22; see also Fig. 162.

?Suborder **RECTANGULATA** Waters, 1887
?Family **LICHENOPORIDAE** Smitt, 1866

Genus ***PARACRESCIS*** nov.

TYPE SPECIES. *Paracrescis boardmani* sp. nov., Faringdon Sponge Gravel, Faringdon, Oxfordshire. See p. 142.

DIAGNOSIS. Colony encrusting, unilamellar or multilamellar, maculate; apertures of autozooecia and apparent alveoli widely spaced, separated by areas of pustulose calcification; maculae lack autozooecial apertures; pseudolunaria may sharply indent outline shape of autozooecial apertures, especially close to maculae; brood chamber cavernous.

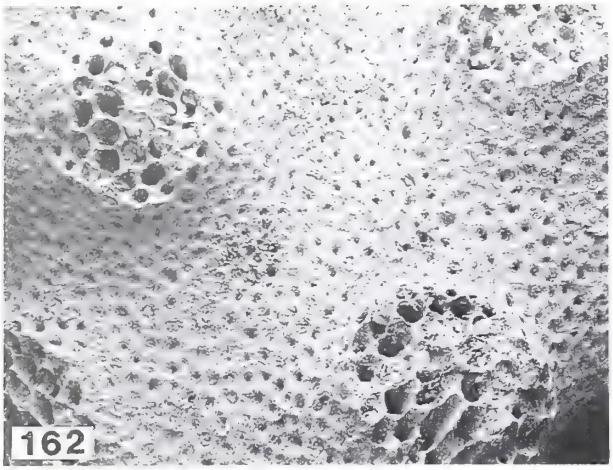
NAME. Somewhat like *Crescis*.

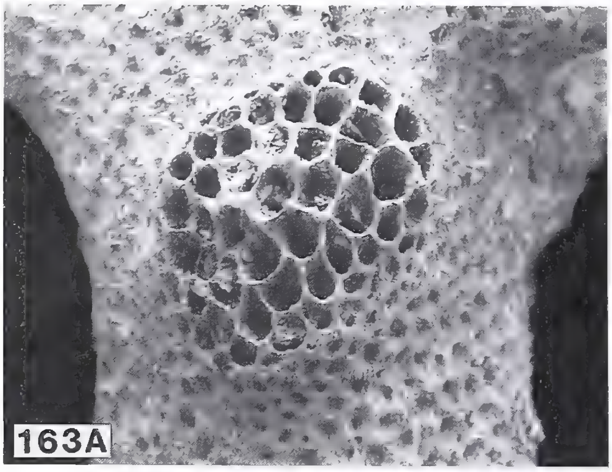
REMARKS. This new monospecific genus is characterized particularly by the wide areas of pustulose calcification which separate the apertures on the colony surface.

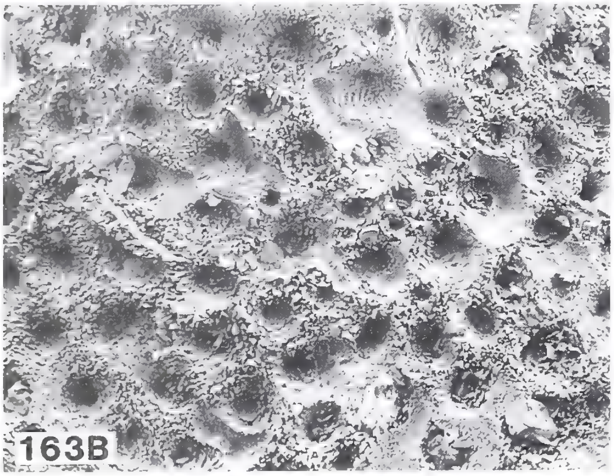
In the presence of pseudolunaria, *Paracrescis* resembles *Semicrescis* d'Orbigny whose type species is *Semicrescis tubulosa* d'Orbigny, 1854 from the Upper Cretaceous of France. External morphology in *S. tubulosa* has not been properly illustrated, but Boardman (1984: fig. 9C–D) has figured thin sections prepared from the type specimen. Boardman's tangential section depicts autozooecia with well-defined pseudolunaria. However, the large apertures are more closely spaced than in *P. boardmani*, and there is no indication of a wide expanse of pustulose calcification between apertures.

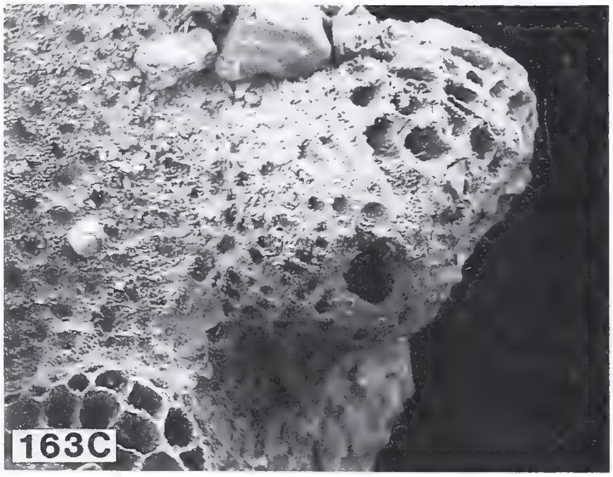
Crescis d'Orbigny is represented by one species, *C. dumetosa* (Lamouroux, 1821) from the M. Jurassic (see Walter 1970). This also has autozooecia with pseudolunaria but lacks the extensive development of pustulose calcification found in *Paracrescis*.

The pustulose calcification and pseudolunaria present in









Figs 162–163 *Echinocava raulinii* (Michelin). Fig. 162, USNM 69903a, × 40; see also Fig. 161. Fig. 163, BM(NH) D57949; 163A, autozooecial fascicle, × 39; 163B, alveoli between fascicles, × 102; 163C, possible broken brood chamber attached to a fascicle, × 48.

Paracrescis are features typifying lichenoporid rectangulates among living cyclostomes. However, the affinity of *Paracrescis* with the Lichenoporidae is difficult to demonstrate in the absence of well-preserved brood chambers. The brood chambers of lichenoporids are roofed by highly perforate interior walls (see Hayward & Ryland 1985). A second possibility is that *Paracrescis* is more closely related to the cerioporine cyclostomes; brood chambers in the similar genus *Crescis* appear to be roofed by pseudoporous exterior wall. Finally, on the basis of the lunaria/pseudolunaria and extrazooidal vesicles, Boardman (1984) believed *Semicrescis*, in which brood chambers are also unknown (E. Voigt, personal communication 1987), to be closely related to the Cystoporata, a stenolaemate order more usually regarded as exclusively Palaeozoic in its distribution.

Paracrescis is here questionably assigned to the Family Lichenoporidae of the Suborder Rectangulata. Accordingly, the small apertures between the autozooecia are labelled as ?alveoli rather than kenozooecia as they would be if *Paracrescis* were assigned to the Cerioporina.

RANGE. Aptian.

Paracrescis boardmani sp. nov. Figs 164–165

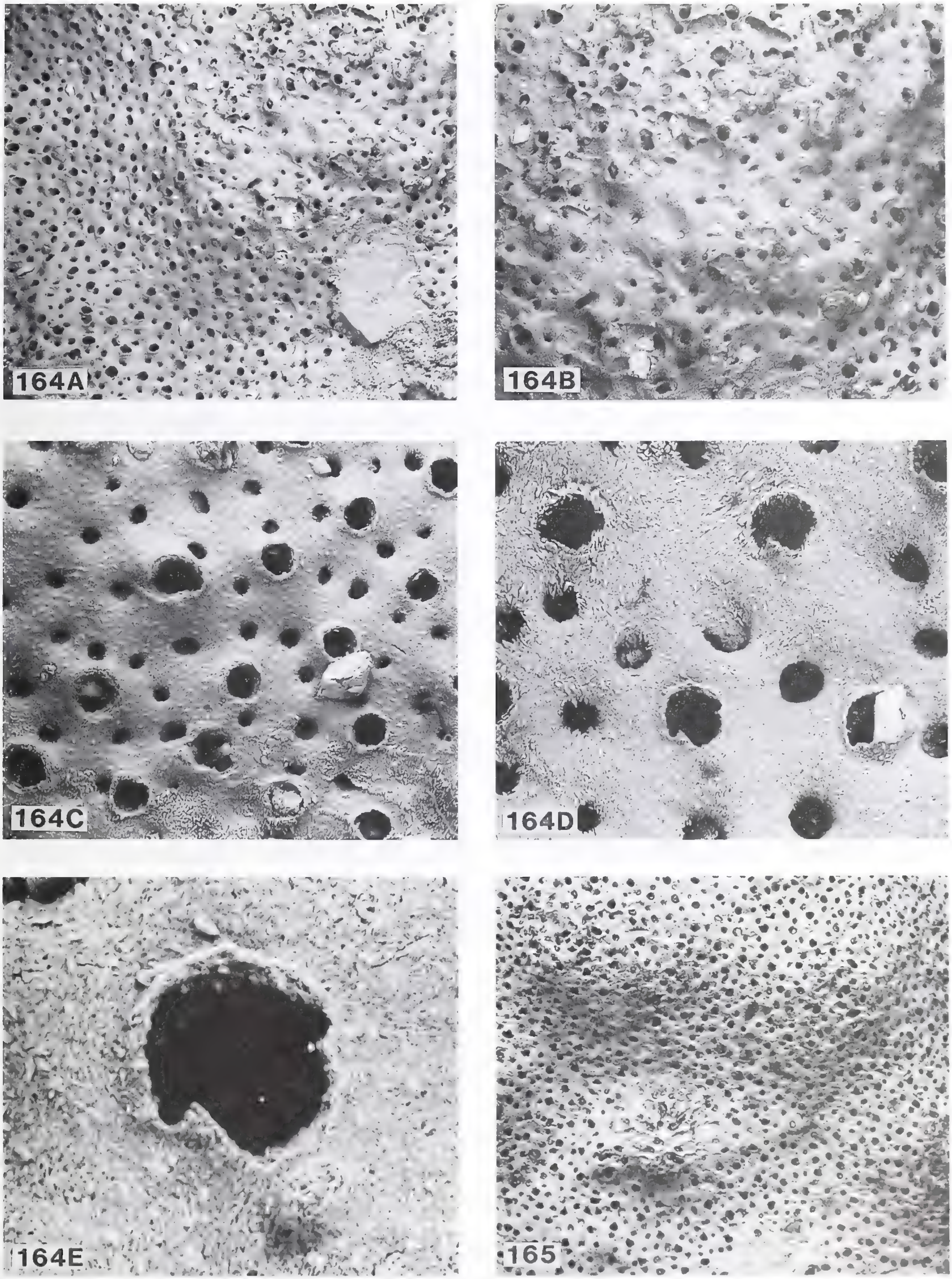
HOLOTYPE. BM(NH) D57711 (specimen and thin section), Little Coxwell Pit, Pitt Colln.

PARATYPES. BM(NH) D57712–3, Little Coxwell Pit, Davis Colln; D58207, west face of Badbury Hill, Faringdon, Pitt Colln.

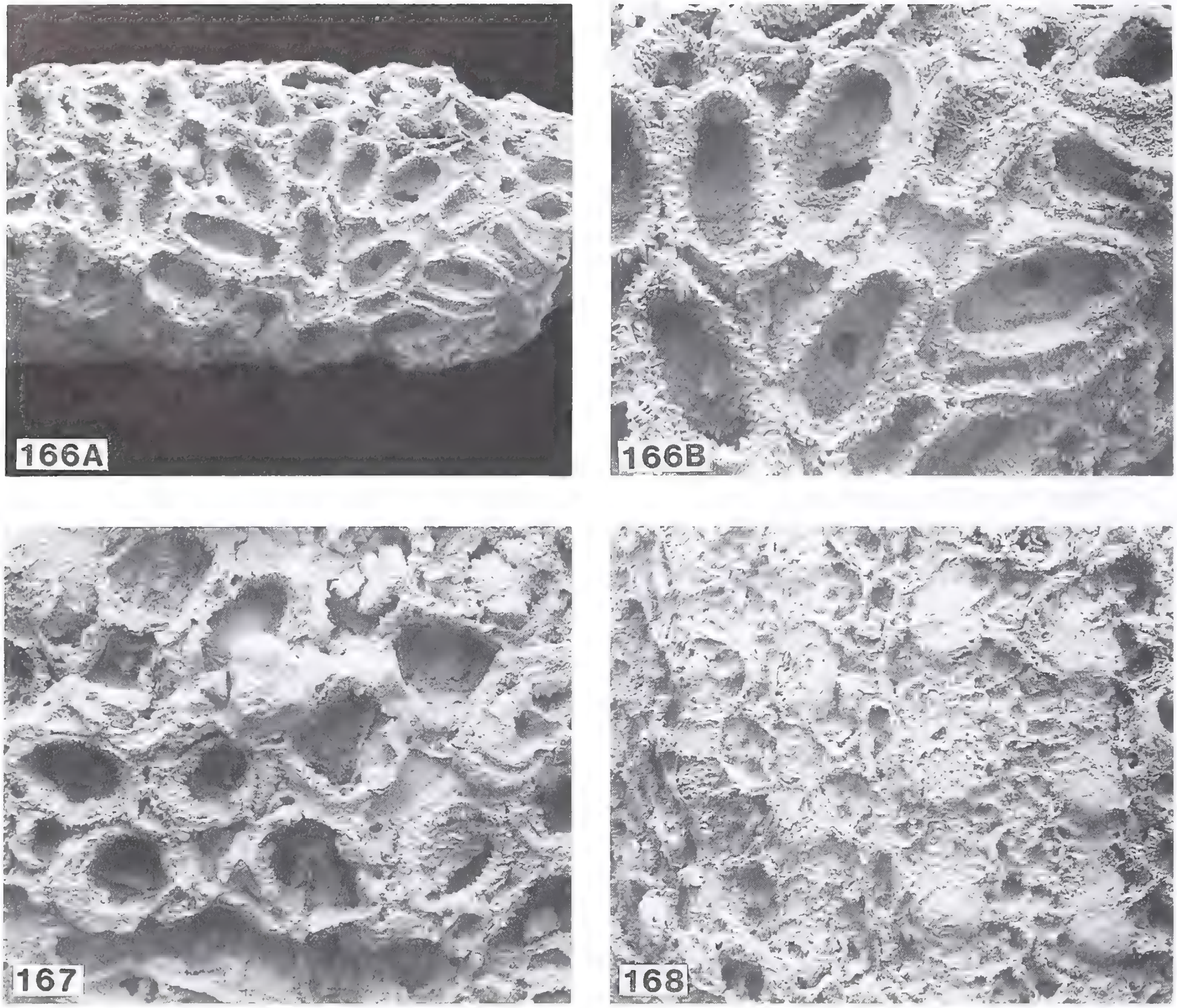
NAME. For R. S. Boardman, in recognition of his major contributions to the study of stenolaemate bryozoans.

DESCRIPTION. Zoarium encrusting, multilamellar with wide spaces often present between successive zoarial layers. The colony surface bears distinct maculae raised as monticules (Figs 164A, 165) and recognizable by their lack of autozooecial apertures and widely spaced ?alveoli. New layers seemingly originate as overgrowths on the flanks of maculae (Fig. 164B). Wide expanses of calcified interior wall, ornamented by small tubercles, occupy the colony surface between autozooecial apertures and ?alveoli (Fig. 164C).

Autozooecial apertures are very small, tending to be larger adjacent to the maculae (Fig. 164C), subcircular to elliptical in shape, with a narrow raised rim which is occasionally



Figs 164–165 *Paracrescis boardmani* sp. nov. Fig. 164, BM(NH) D57711, **holotype**; 164A, maculum (top right) and surrounding intermacular area, × 22; 164B, maculum with developing overgrowth (top), × 39; 164C, zooecia and ?alveoli at edge of maculum (note tubercles ornamenting walls), × 86; 164D, zooecial apertures and ?alveoli, × 170; 164E, autozooecial aperture with well-developed pseudolunarium, × 550. Fig. 165, BM(NH) D57712, worn, mammilate colony surface, × 18.



Figs 166–168 *Charixa lhuydi* (Pitt). Fig. 166, BM(NH) D55068; 166A, × 39; 166B, detail of cement encrusted zooecia, × 104. Fig. 167, BM(NH) D54167, typical irregular arrangement of zooecia, × 50. Fig. 168, BM(NH) D54191, part of a worn colony encrusting an echinoid spine, showing a row of three caudate zooecia following a vertical groove in the spine (centre), × 34.

developed into a pseudolunarium (Fig. 164D, E) sharply indenting the proximal edge of the aperture, particularly in zooecia close to maculae. The widely spaced apertures are arranged more-or-less in quincunx in intermacular areas.

Apparent alveoli (Fig. 164D) have small, sunken apertures with inwardly-sloping sides, and are about 0·02–0·03 mm in diameter.

Brood chamber, only observed fractured in one poorly-preserved specimen (D58207), is cavernous and is pierced by autozooecia which apparently support the roof.

In tangential section the zooecial walls are thick, and indistinctly laminated or granular in appearance, with clearer linings visible in some of the autozooecia.

Measurements. LAM, mean 0·06 mm; TAM, mean 0·05 mm.

Remarks. *P. boardmani* is clearly distinguished from other early Cretaceous cyclostomes by the pustulose frontal calcification and pseudolunaria. There is a slight resemblance to the Valanginian species *Reptocavea rugosa* d'Orbigny, 1853, revised by Cotillon & Walter (1965; see also Walter 1972, Walter *et al*. 1975) as *Petalopora rugosa* (d'Orbigny), but this lacks these two characteristic features, and has autozooecial apertures about twice the size of those in *P. boardmani*.

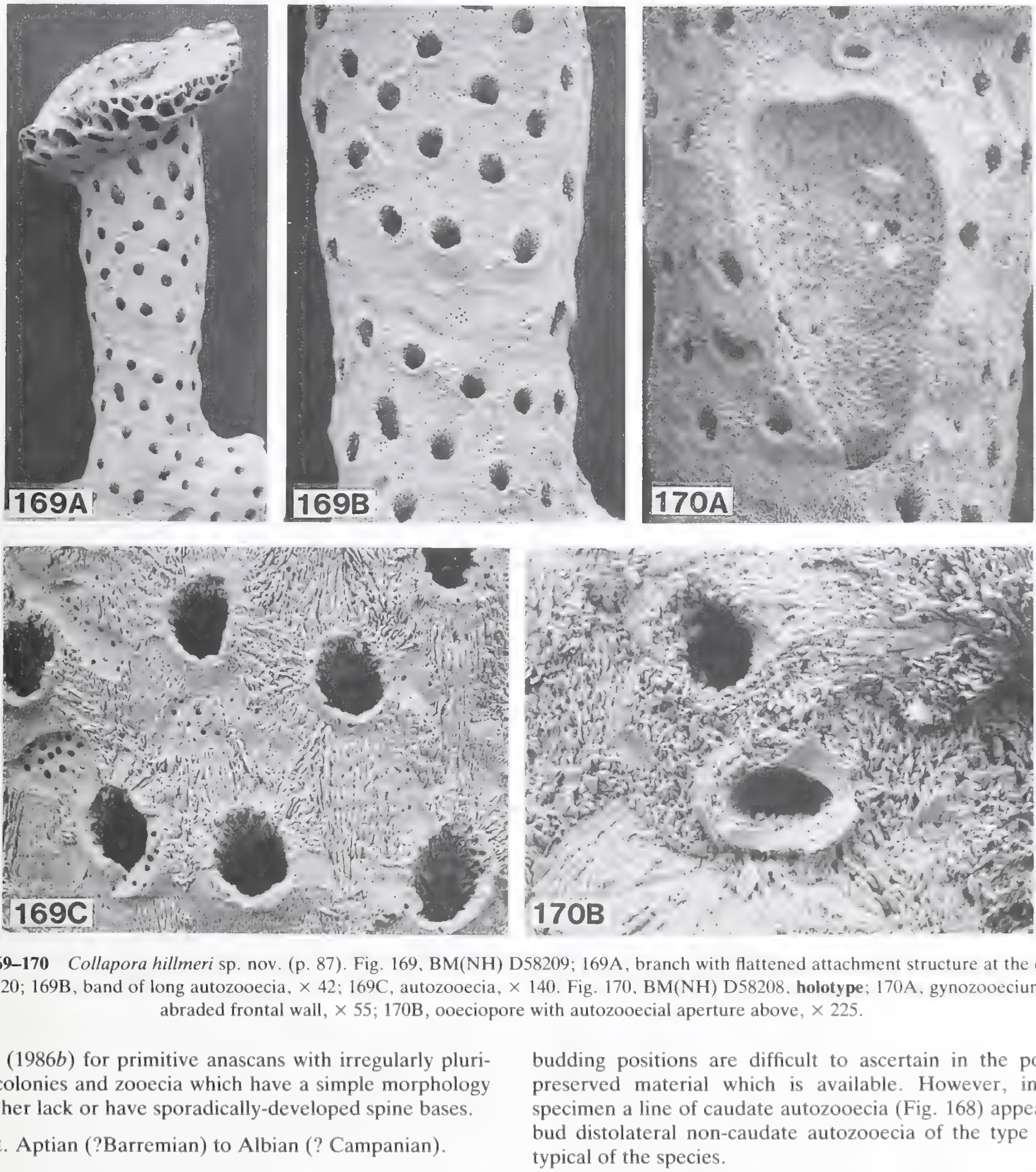
Only four specimens are known of *P. boardmani*. The holotype is a small colony encrusting a branch of an erect cyclostome, while one of the paratypes (BM(NH) D57712) is a large, hollow, flabellate colony which apparently encrusted an erect soft-bodied organism.

Class **GYMNOLAEMATA** Allman, 1856
Order **CHEILOSTOMATA** Busk, 1852
Suborder **ANASCA** Levinsen, 1909

Genus ***CHARIXA*** Lang, 1915

Type species. *Charixa vennensis* Lang, 1915, by original designation; Albian, Dorset.

Remarks. The genus *Charixa* is used in accordance with



Figs 169–170 *Collapora hillmeri* sp. nov. (p. 87). Fig. 169, BM(NH) D58209; 169A, branch with flattened attachment structure at the distal end, × 20; 169B, band of long autozooecia, × 42; 169C, autozooecia, × 140. Fig. 170, BM(NH) D58208, **holotype**; 170A, gynozooecium with abraded frontal wall, × 55; 170B, ooeciopore with autozooecial aperture above, × 225.

Taylor (1986*b*) for primitive anascans with irregularly pluriserial colonies and zooecia which have a simple morphology and either lack or have sporadically-developed spine bases.

RANGE. Aptian (?Barremian) to Albian (? Campanian).

Charixa lhuydi (Pitt, 1976) Figs 166–168

1976 *'Membranipora' lhuydi* Pitt: 65; pl. 1, figs A–D.
1986*b* *Charixa lhuydi* (Pitt) Taylor: 203; figs 4, 5.

HOLOTYPE. BM(NH) D52494, Little Coxwell Pit, Pitt Colln.

PARATYPE. BM(NH) D52495, Little Coxwell Pit, Pitt Colln.

OTHER MATERIAL. BM(NH) D54190–200, Hinde Colln; D55067, Little Coxwell Pit, Davis Colln; D55068, Little Coxwell Pit, Elliott Colln.

DESCRIPTION. Colonies are encrusting and comprise irregular pluriserial patches of zooecia (Fig. 166A) which sometimes show multilamellar overgrowth. Zooecial orientations and budding positions are difficult to ascertain in the poorly-preserved material which is available. However, in one specimen a line of caudate autozooecia (Fig. 168) appears to bud distolateral non-caudate autozooecia of the type more typical of the species.

Autozooecia are usually elliptical in outline (Fig. 168B) and have a slight proximal gymnocyst. Rarely, autozooecia are pyriform and have a caudate proximal gymnocyst about half the length of the zooecium. In the holotype, autozooecial length averages 0·44 mm and width 0·33 mm. Opesiae are elongate elliptical and occupy most of the frontal surface of the majority of autozooecia. Cryptocysts are usually obscured by calcite cement but appear to be steeply sloping and seem to be pustulose. Unequivocal closures and regenerations have not been observed.

Communication pores are present as windows in vertical walls (see Pitt 1976: pl. 1, fig. D), but the expected presence of pore chambers has not been confirmed in this poorly-preserved material.

Some of the irregular spaces between autozooecia appear to be occupied by kenozooecia with extensive opesiae. These were perhaps misidentified by Pitt (1976) as broken ovicells. Avicularia and unequivocal ovicells are absent. The ancestrula is unknown.

MEASUREMENTS. Zooecial length 0·36–0·45 mm, mean 0·41 mm; zooecial width 0·20–0·35 mm, mean 0·25 mm.

REMARKS. This is the only cheilostome species known from Faringdon, and one of relatively few early Cretaceous cheilostomes described from anywhere in the world (Taylor 1986*b*). Since Pitt's (1976) original description of this species several additional specimens have become available, but unfortunately these share the poor preservation of the holotype and paratype. A considerable growth of calcite cement obscures surface details, and several colonies are abraded (e.g. Fig. 167). However, the finding of a colony with a line of caudate autozooecia (Fig. 168) prompts assignment of the species to *Charixa* Lang, 1915 (type species *C. vennenensis* from the Albian of Dorset). These caudate autozooecia follow a furrow in the echinoid spine encrusted by the colony. Their distolateral buds appear to be non-caudate autozooecia of the kind which predominate in *C. lhuydi* colonies. By comparison with *Spinicharixa dimorpha* (see Taylor 1986*b*), it is thought that the caudate autozooecia represent an initial runner-like growth across the substrate.

With one exception, all known specimens encrust regular echinoid spines. Colonies often occupy the entire circumference of the spine and are usually absent from the collar region. Spines of Recent echinoids are frequently fouled by epizoans (including bryozoans) while the echinoid is still alive (Mortensen 1928: 27), but remain free of encrusters on the collars of the spines where muscles attaching the spine to its base are situated. Therefore, it appears possible that *C. lhuydi* was a life associate of echinoids, though the single colony (D55068) encrusting an erect branch of the cyclostome *Meliceritites* shows that the association was not entirely obligatory for *C. lhuydi*.

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GLOSSARY

This terminological glossary is included for two reasons: firstly, many terms in bryozoology are unfamiliar to the non-specialist; and secondly, there is no consensus of opinion among bryozoologists about the definition of many terms (see Boardman *et al.* 1983: 304).

Adnate: Encrusting, closely cemented to a substrate.

Ancestrula: The founding zooid of the colony formed by settlement and metamorphosis of the larva.

Alveoli: Apparent interzooidal spaces between the autozooecia in rectangulate cyclostomes which are enclosed by interior wall calcification.

Aperture: The opening at the distal end of the zooecium through which the tentacle crown is protruded (in cheilostomes, 'aperture' is sometimes used in place of 'opesia').

Astogeny: The development of the colony.

Astogenetic zones: Developmental zones of the colony which are distinguished by the morphology of their constituent zooids: progressive elaboration of zooid morphology and, usually, increase in zooid size occurs distally through zones of astogenetic change, including a zone of primary astogenetic change around the colony origin; zones of astogenetic repetition contain zooids of similar morphology (excepting polymorphic, ontogenetic and ecophenotypic differences).

Atrial ring: A ring-like ridge located inwards of the ooeciopore in melicerititid gynozooecia.

Autozooecium: The skeleton of an inferred feeding zooid.

Avicularium: Cheilostome polymorph with a modified operculum and orifice.

Basal lamina: The basal calcified layer of a cyclostome colony usually closely adnate to the substrate but occasionally becoming free.

Bereniciform: An adnate, single-layered, multiserial fan-like to discoidal colony-form in cyclostomes (see Taylor 1976: text-fig. 2).

Bifoliate: Erect colony construction with two layers of zooids back-to-back.

Brood chamber: Any chamber for the brooding of larvae; includes cyclostome gynozooecia and so-called zoarial brood chambers, and cheilostome ovicells.

Cancelli: Small pits on the surface of cancellate cyclostome colonies which may be kenozooids or interzooidal spaces.

Colony: The aggregate of zooids (and any extrazooidal parts) derived from a single larva.

Cryptocyst: Interior body wall calcification (grown beneath a covering of soft tissue), often pustulose, which may contribute to the frontal wall of the cheilostome zooid surrounding the opesia and surrounded by the gymnocyst.

Dendroid: An erect, tree-like branching pattern.

Diaphragm: A horizontal plate partitioning or sealing the zooecium in cyclostomes. Basal diaphragms are secreted from the oral side and form a floor to the living chamber of the zooid. Terminal diaphragms are secreted from the aboral side and occlude the zooecium close to the level of the aperture.

Dichotomous branching: Symmetrical branch bifurcation.

Eleozooecium: Polymorph of melicerititid cyclostomes in which the aperture and operculum is modified.

Endozone: The inner zone of a massive or erect colony composed of the thin-walled proximal parts of the zooecia typically orientated subparallel to branch growth direction.

Exozone: The outer zone of a massive or erect colony composed of the thick-walled distal parts of the zooecia typically orientated subperpendicular to branch growth direction.

Fascicle: A bundle of autozooecial apertures.

Frontal wall: A wall on the frontal surface of the zooid which is parallel or subparallel to the colony growth direction.

Gymnocyst: Exterior body wall calcification (cuticle-covered during life) in cheilostome zooids which commonly forms the zooidal vertical walls and may contribute to the frontal wall.

Gynozooecium: A polymorph formed by a single fertile zooid used to brood larvae in many cyclostomes; gynozooecia generally have bulbous distal parts in which the frontal wall bears a higher density of pseudopores than in the autozooecia, and apertures (ooeciopores) smaller than autozooecial apertures. Synonymous with gonozooecium as commonly used.

Kenozooecium: The skeleton of an inferred kenozooid, a polymorph lacking functional gut and tentacles, and usually smaller than an autozooid; in tubuloporine cyclostomes kenozooecia usually have frontal walls without apertures.

Lateral branching (or ramification): When daughter branches arise from the sides of existing branches, typically at about 90° to the parent branch and sometimes proximally of the branch growth tip.

Maculum: A distinct patch on the colony surface, usually marking the site of an excurrent chimney, often formed by a cluster of polymorphs or new zooecial buds.

Moniliform: Term used to describe zooecial walls (in thin section) with periodic thickenings.

Monticule: A hummock on the colony surface which probably formed an excurrent chimney.

Multilamellar: Multilayered colony construction achieved by self-overgrowth.

Mural spines (= intrazooecial spines): Small spines projecting inwards from the walls of the zooecia in cyclostomes; often visible inside zooecial apertures.

Ontogeny: The development of a zooid (cf. astogeny).

Operculum: A hinged plate which closes the cyclostome aperture or cheilostome orifice when the tentacles are retracted; opercula are rarely calcified in cheilostomes; among cyclostomes, opercula are present only in the Family Eleidae (melicerititids) in which they are calcified.

Orifice: The opening, closed by the operculum, in cheilostomes which allows the tentacle crown access to the exterior.

Opesia: The uncalcified 'window' on the frontal surface of a cheilostome zooid; during life, it is occupied by the frontal membrane and the operculum.

Ovicell: Small calcified larval brood chamber immediately distal of the orifice of the maternal zooid in cheilostomes.

Peristome: A tubular prolongation around the zooecial aperture.

Probosciniform: An adnate, oligoserial, ribbon-like growth-form in cyclostomes (see Taylor 1976: text-fig. 2).

Protoecium: The bulb-like proximal part of a cyclostome ancestrula.

Pseudolunarium: A hood-like spine or shield projecting above the surface of the aperture or indenting the outline of the aperture on its proximal side in some rectangulate cyclostomes.

Pseudopores: Minute pores present in the frontal, calcified exterior walls of cyclostomes which are cuticle-covered during life.

Vinculariiform: Colony growth-form, originally applied to cheilostomes, in which the rigidly erect and bush-like colony consists of narrow, bifurcating branches.

Zoarium: The skeletal remains of a colony.

Zooecium: The skeletal remains of a zooid.

Zooid: The modular unit of a bryozoan colony, homologous with the individual in a unitary animal.

IDENTIFICATION KEY

Identification of many of the Faringdon bryozoan species is difficult. This is particularly true of the bereniciform tubuloporines (species of *Plagioecia, Hyporosopora, Mesonopora* and '*Berenicea*') in which the slight differences between some species can only be appreciated by direct comparison of specimens. The common absence of gynozooecia also provides a problem when trying to identify species; therefore, gynozooecial characters have been omitted from this key, but they can be found in the species descriptions. Furthermore, poorly preserved material which is abraded, or obscured by calcite cement may be impossible to determine. Identifications made using this key should be carefully checked against the full descriptions and illustrations of the species.

1.	Zoaria encrusting or massive	2
	Zoaria erect	30
2.	Branching colony-form	3
	Sheet-like colony-form	13
3.	Branches uniserial or partly biserial	4
	Branches multiserial ('ribbon-like')	8
4.	Branches zig-zag with zooecia facing alternately to left and right	***Stomatoporina alternata***
	Otherwise	5
5.	Zooecia narrow (width <0·2 mm)	6
	Zooecia broad (width >0·2 mm)	7
6.	Branches bifurcating	**Stomatoporid sp. 2**
	Branches with lateral ramifications	**Stomatoporid sp. 1**
7.	Zooecia barrel-like, narrowing distally	***Voigtopora calypso***
	Zooecia parallel-sided; branches sometimes biserial following bifurcation	***'Stomatopora' melvillei***
8.	Branches of low profile, flat-topped or gently convex	9
	Branches of high profile, distinctly arched or ridged	12
9.	Zooecial apertures >0·10 mm	10
	Zooecial apertures <0·10 mm	11
10.	Branches with border of kenozooecia; lateral ramifications sometimes present	***Proboscinopora marginata***
	Branches lacking border of kenozooecia	***Oncousoecia depressa***
11.	Zooecia minute (<0·4 mm long); frontal walls convex; apertures often longitudinally elongate	***Oncousoecia parvula***
	Zooecia larger (<0·8 mm long); frontal walls flat; apertures often transversely elongate	***Oncousoecia coarctata***
12.	Zooecia broad (>0·15 mm wide); branches wide with rounded cross sections	***Idmonea radiolitorum***
	Zooecia narrow (<0·15 mm wide); branches subtriangular in cross section; lateral ramifications may occur	***Idmonea denticulata***
13.	Zooecia ovoidal or caudate, irregularly and loosely arranged; apertures (opesiae) extensive	***Charixa lhuydi***
	Otherwise	14
14.	Zooecia without frontal walls	15
	Zooecia with frontal walls	18
15.	Large multilayered zoaria composed of numerous	

inverted cup-shaped subcolonies ..... ***Semimulticavea marginata***
Otherwise 16

16. Zooecia monomorphic; zoaria thick, often with knobbly branches; maculae absent .. ***Ceriopora farringdonensis***
Zooecia dimorphic 17

17. Apertures separated by wide areas of calcification; pseudolunaria present in some autozooecial apertures. ***Paracrescis boardmani***
Apertures closely spaced; centres of maculae devoid of autozooecia ..... ***Seminodicrescis variolata***

18. Apertures opening on frontal surface of zoaria 19
Apertures opening only at distal growing edge; typically small, thick zoaria ..... ***Hyporosopora larwoodi***

19. Apertures opening on prominent ridges which are separated by low-lying areas of kenozooecia lacking apertures ..... ***Reptoclausa hagenowi***
Otherwise 20

20. Apertures connate, aligned in radial rows ..... ***Unitubigera* sp.**
Otherwise 21

21. Apertures 8-shaped; constricted medially by a group of mural spines ..... ***Hyporosopora constricta***
Otherwise 22

22. Apertures absent from centre of zoaria, crowded at the distal edge ..... ***Hyporosopora larwoodi***
Otherwise 23

23. Apertures very closely spaced; zooecia short; maculae may occur in which zooecia are longer than average ... ***Plagioecia spissa***
Apertures spaced well apart 24

24. Apertures >0·15 mm in diameter 25
Apertures <0·15 mm in diameter 26

25. Zooecia flask-shaped, their frontal walls convex; zoaria lobate ..... ***'Berenicea' grandipora***
Zooecia immersed ..... ***'Berenicea' faringdonensis***

26. Apertures distantly spaced, 0·12–0·13 mm in diameter; zoaria unilamellar ..... ***'Berenicea' filifera***
Otherwise 27

27. Zoaria composed of discoidal subcolonies 28
Otherwise 29

28. Zoaria thin; zooecial frontal wall width >0·10 mm ..... ***'Berenicea'* cf. *sowerbyi***
Zoaria thick, several generations of buds visible at the growing edge; zooecial frontal wall width <0·10 mm... ***Mesonopora fecunda***

29. Apertures lacking peristomes or apertural rims; zoaria often with a lustrous surface ... ***Hyporosopora mantelli***
Apertures with well-defined rims .... ***Plagioecia orbifera***

30. Bilamellar fronds ..... ***?Mesenteripora campicheana***
Otherwise 31

31. Zooecia with frontal walls 32
Zooecia lacking frontal walls 40

32. Zooecia opening all around branch circumference 33
Zooecia opening on one side only of branches which are short and have not been observed to bifurcate ..... ***Filisparsa gasteri***

33. Apertures with a straight proximal edge; opercula may be present 34
Apertures circular or elliptical 37

34. Apertures small, <0·10 mm in transverse diameter; branches often <1 mm in diameter ..... ***Meliceritites dendroidea***
Apertures >0·10 mm in transverse diameter 35

35. Apertures appreciably higher than wide, distinctly arch-shaped and flared with a deep distal ledge ..... ***Meliceritites gracilis***
Otherwise 36

36. Apertures >0·15 mm in transverse width, closely spaced; branches thick, usually >1·5 mm in diameter ..... ***Meliceritites cunningtoni***
Apertures <0·15 mm in transverse width; branches usually <1·5 mm in diameter ..... ***Meliceritites transversa***

37. Branches narrow (generally <1 mm), subcircular in cross section, lacking a median budding lamina 38
Branches >1 mm in diameter, compressed, with a median budding lamina 39

38. Gynozooecia with lobes extending distally of a compressed ooeciopore; kenozooecia commonly interspersed among autozooecia ..... ***Entalophoroecia quadripartita***
Otherwise ..... ***Collapora hillmeri***

39. Apertures *c.* 0·08 mm in diameter; frontal walls delicate; branches usually <2 mm in diameter .. ***Ceata granulata***
Apertures 0·10–0·16 mm in diameter; frontal walls robust; branches generally 2–3 mm in diameter ..... ***Cardioecia neocomiensis***

40. Zoaria seldom branching, composed of numerous stacked subcolonies 41
Otherwise 44

41. Zooecia dimorphic, thin-walled 42
Zooecia monomorphic, thick-walled ..... ***Reptomulticava brydonei***

42. Autozooecia arranged in well-defined radial rows 43
Autozooecia not arranged in clearly-defined rows; apertures 0·06–0·08 mm in diameter . ***Tholopora hastingsae***

43. Autozooecial apertures >0·15 mm in diameter ..... ***Tholopora thomasi***
Autozooecial apertures 0·08–0·10 mm in diameter ..... ***Tholopora dightoni***

44. Autozooecial apertures arranged in circular fascicles raised above the surrounding branch surface ..... ***Echinocava raulinii***
Autozooecial apertures not in fascicles 45

45. Branches <4 mm in diameter 46
Branches >4 mm in diameter 51

46. Kenozooecia absent or very few; branches with median budding lamina ..... ***Ceata granulata*** (abraded state)
Kenozooecia abundant 47

47. Autozooecial apertures opening on one side only of branches; branches narrow, commonly *c.* 0·6 mm in diameter ..... ***Siphodictyum gracile***
Autozooecial apertures not so restricted 48

48. Autozooecial apertures opening on 2 faces of the branches separated by strips of kenozooecia 49
Otherwise 50

49. Branches >1·4 mm in diameter, compressed in cross section ..... ***Laterocavea dutempleana***
Branches <1 mm in diameter, subcircular in cross section ***Laterocavea? intermedia***

50. Autozooecial apertures <0·09 mm in diameter with

distinct rims; branches <1·5 mm in diameter; kenozooecial apertures funnel-shaped .... ***Tetrocycloecia multiporosa***
Autozooecial apertures >0·09 mm in diameter; branches >1·5 mm in diameter; kenozooecia sometimes occluded .... ***Clausa zonifera***

51. Zooecia monomorphic; maculae absent; branches may be >20 mm in diameter .... ***Ceriopora farringdonensis***
Zooecia dimorphic or weakly so; branches usually <15 mm in diameter 52

52. Well-developed maculae devoid of autozooecial apertures; bifurcating branches ...... ***Heteropora keepingi***
Maculae absent; branches clavate, commonly with overgrowths .... ***Heteropora clavata***

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